ECOLOGICAL INTERACTIONS AMONG IMPORTANT GROUNDFISHES IN THE GULF OF ALASKA

By

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Abstract

Complex ecological interactions such as predation and competition play an important role in shaping the structure and function of marine communities. In fact, these processes can have greater impacts than those related to fishing. We assessed ecological interactions among economically important fishes in the Gulf of Alaska – a large marine ecosystem that has recently undergone considerable shifts in community composition. Specifically, we developed an index of predation for Walleye Pollock (*Gadus chalcogrammus*) to examine spatiotemporal changes in consumption, quantify portfolio effects, and better understand diversity-stability relationships within the demersal food web. We also evaluated the potential for competition between two important pollock predators, Arrowtooth Flounder (*Atheresthes stomias*) and Pacific Halibut (*Hippoglossus stenolepis*). We found highly variable predation intensity on Gulf of Alaska pollock. The combination of a single dominant predator and synchronous consumption dynamics indicated strong top-down control in the region. Spatial heterogeneity, however, may offset trophic instability at the basin scale. Assessments of resource partitioning provided little indication for competition between Arrowtooth Flounder and Pacific Halibut of similar lengths. Morphological differences between the two flatfish predators prompted an exploration into whether our conclusions about resource partitioning were dependent upon the size metric used. From this study, we found a relatively early onset of piscivory for Arrowtooth Flounder. Relationships between predator size and prey size also suggested gape limitation among Pacific Halibut sampled. Trophic niche separation was more pronounced for fishes with larger gapes, indicating greater potential for competition among smaller Arrowtooth Flounder and Pacific Halibut in Southeast Alaska. Reexamining basin-scale relationships between spatial and dietary overlap according to gape size would further elucidate the effects an increasing Arrowtooth Flounder population has had on changes in Pacific Halibut size-at-age. Results from this

dissertation improve our understanding about the impacts of complex ecological interactions on population and community dynamics, and how those interactions may change in time, space, and under different environmental conditions.

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General Introduction

Complex ecological interactions, such as predation and competition, play an important role in shaping the structure, function, and stability of marine communities (Sih *et al.* 1985; Hixon and Jones 2005; Gamble and Link 2009). In some cases, these processes can have greater impacts on the demography of harvested species than removals from fishing (Bax 1991; Christensen and Pauly 1993; Tyrrell *et al.* 2011). Predation tends to exhibit greater control over lower trophic levels (*e.g.,* herbivores and primary carnivores), whereas competition is more important among higher trophic-level predators (Hairston *et al.* 1960; Menge and Sutherland 1976; Sih *et al.* 1985). Both types of ecological interactions can lead to a reduction in niche breadth (*e.g.,* restricted use of habitat, more limited types of prey consumed) for one or more species. When scaled to the community level, food web interactions can have a myriad of effects, such as shifting the degree of predatory control experienced by prey populations (*e.g.,* Oken *et al.* 2018) or limiting growth rates within the predator assemblage (*e.g.*, Hanson and Leggett 1985). Thus, it is important to identify and quantify ecological drivers of population abundance, especially for species of considerable economic or cultural value. For instance, estimates of predation mortality can be used as an intermediary between conventional single species assessments and ecosystem-based fisheries management, whereas competition studies can inform about the population dynamics of important fish stocks.

Although highly variable in time and space, predation remains the greatest source of mortality for juvenile and lower trophic-level fishes (Bax 1991). Cumulative effects of predation may be direct, such as driving recruitment dynamics of prey populations through increased mortality of specific year classes (Bax 1998; Christensen 1996). Effects may also be indirect and trait-mediated (*e.g.*, Peacor and Werner 2001), manifesting as changes in prey behavior that result in reduced access to suitable resources and subsequently

decreased growth and/or reproduction (MacArthur 1972; Colwell and Fuentes 1975; Bax 1998). Predation risk may be mediated, however, through rapid growth (*i.e.*, outgrowing predator gape limitations), morphological defenses (*e.g.,* spines), relatively fast swimming speeds (to reduce capture efficiency), or occupying refuge habitats that are inaccessible to predators (Juanes 1994). Although intense predation often yields deleterious results for consumed populations, increased predation on locally abundant prey may reduce competition among lower trophic levels (*e.g.,* Overholtz *et al.* 1999; Garrison and Link 2000).

Ecological effects on upper trophic levels are less frequently attributed to predation. Rather, relatively large-bodied animals must find ways to alleviate the negative effects of competition (Schoener 1983; Ross 1986). There are two basic types of competition that result when organisms attempt to utilize the same limited resources in similar ways. Interference competition takes place when one individual, population, or species possesses an inherent trait or displays a behavior that prevents another from utilizing a particular resource (Schoener 1983). Exploitative competition occurs when an individual, population, or species uses one or more resources in a way that reduces the availability of that resource for other species. Both forms of competition inevitably result in a shift or reduction in the niche breadth of one or more competitors (Colwell and Futuyama 1971; Colwell and Fuentes 1975; Hixon and Jones 2005). Long-term effects may include reduced growth, reproductive potential, and/or survival of the inferior competitor (*e.g.,* Hanson and Leggett 1985; Persson 1990; Carpenter 2005).

Predation and competition are pervasive in ecology. However, the complex and variable nature of these interactions make it difficult to estimate and predict their effects (Bax 1998), particularly in large marine ecosystems. Quantifying predation and competition involves multifaceted analyses that are often nonlinear, multivariate, and include many different

scales (Ostrom 2007). Accurately estimating predation mortality necessitates biomass, consumption rate, and diet composition information for all major predators. Assessing the potential for competition is also data intensive, requiring an understanding about resource availability, population trajectories, resource overlap between likely competitors, and the role of size in determining competitive superiority (Piet *et al.* 1998, Link 2002, Link and Auster 2013). When information about resource availability is limited, which is often the case in open marine systems, we can employ the limiting similarity hypothesis. This hypothesis asserts that there is a maximum degree of niche overlap that allows for continued coexistence of multiple species (MacArthur and Levins 1967; Pianka 1974). Niche complementarity (*i.e.,* the expected negative relationship between resource overlap along two dimensions) can then be used as a measure of resource partitioning between species that are thought to compete (Schoener 1974; Pianka 1980; Ross 1986).

Adding to the difficulties associated with quantifying predation and competition is the fact that ecological interactions are not static in time or space (Bax 1998, Hunsicker *et al.* 2013). Moreover, the scale of data collection and analyses may not match the scale at which ecological interactions are operating, affecting our interpretations about population or community dynamics (Levin 1992; Hunsicker *et al.* 2011; Link and Auster 2013). Thus, estimates of predation and competition must account for spatiotemporal heterogeneity and deal with issues of scale to accurately estimate the direction and magnitude of their effects on population and community dynamics.

The Gulf of Alaska is an excellent system within which to study spatiotemporal patterns in predation and competition. First, this large marine ecosystem has undergone considerable shifts in community composition over the past few decades. The dynamic and unpredictable nature of this system has been attributed, at least in part, to increased predator biomass over the past few decades (*e.g.*, Gaichas *et al.* 2015). Arrowtooth

Flounder, in particular, exhibited a nearly five-fold increase between the 1960s and early 2010s. Notably, however, Pacific Cod (*Gadus macrocephalus*) biomass declined by 79% following a widespread marine heatwave in the North Pacific (Barbeaux *et al.* 2018; Zador and Yasumiishi 2018). Walleye Pollock (*Gadus chalcogrammus*), which support some of the world's largest fisheries and serve as important prey for a wide variety of species (including Arrowtooth Flounder and Pacific Cod), have also experienced sizeable fluctuations in abundance through time (Dorn *et al.* 2017).

In addition to temporal change associated with community reorganization, the Gulf of Alaska encompasses an assortment of geographic features and environmental conditions that generate considerable spatial heterogeneity. The western Gulf of Alaska is characterized by a relatively wide continental shelf, cool water temperatures, high primary productivity, elevated groundfish abundances, and lower species diversity when compared to the eastern portion of the region (Mueter and Norcross 2002; Zador and Yasumiishi 2018). This broad-scale spatial heterogeneity, when combined with remarkable shifts in community composition, provide an excellent opportunity to further our understanding about ecological associations within the groundfish assemblage. Spatially-expansive, long-term, and multifaceted survey data make it possible to estimate prey consumption and resource partitioning at community and population levels, aiding in the evaluation of predation and competition at broad spatiotemporal scales that are useful for fisheries management and potentially most relevant to highly mobile groundfish species.

In this dissertation, I use a variety of data sources to explore the effects of predation and competition on economically and/or ecologically valuable species in the Gulf of Alaska. Three distinct chapters focus on five groundfish predators: Arrowtooth Flounder (*Atheresthes stomias*), Pacific Cod (*Gadus macrocephalus*), Pacific Halibut (*Hippoglossus stenolepis*), Sablefish (*Anoplopoma fimbria*) and Walleye Pollock conspecifics. Each

component involved extensive collaborations; thus, I elected to use the "we" pronoun when describing methods, results, and interpretations. Manuscript coauthors (*i.e.,* project-specific "we") are listed in the footnote at the beginning of each chapter. In Chapter 1, we calculated spatiotemporal variation in consumption of Walleye Pollock and used this index of predation to better understand diversity-stability relationships in the demersal Gulf of Alaska food web. An additional outcome of this project was to link ecological information (*e.g.,* estimates of predation mortality) directly to the regional stock assessment for pollock in an effort to provide ecosystem-based biological reference points for fisheries management (*sensu* Dolan *et al.* 2016). For Chapters 2 and 3, we evaluated resource partitioning as an indicator of competition between two pollock predators – Pacific Halibut and Arrowtooth Flounder. Fisheries stakeholders and resource managers identified competition with an increasing Arrowtooth Flounder population as a potential mechanism for reduced size-at-age of Pacific Halibut. In Chapter 2, we relied on standardized bottom trawl survey and food habits data to quantify spatial and dietary overlap throughout the Gulf of Alaska. Whereas Chapter 2 focused on estimating niche complementarity among fishes with similar fork lengths, Chapter 3 investigated the role of size (both body and gape) in dietary partitioning between Pacific Halibut and Arrowtooth Flounder from nearshore Southeast Alaska.

Chapter 1 Development of a predation index to assess trophic stability in the Gulf of Alaska [1]

1.1 Abstract

Predation can have substantial and long-term effects on the population dynamics of ecologically important prey. Diverse predator assemblages, however, may produce stabilizing (*i.e.,* 'portfolio') effects on prey mortality when consumption varies asynchronously among predators. We calculated spatiotemporal variation in predation on a dominant forage species to quantify portfolio effects in a food web context and better understand diversity-stability relationships in a large marine ecosystem that has undergone considerable changes in community composition. We selected Walleye Pollock (*Gadus chalcogrammus*) as our focal species because they support some of the largest, most valuable commercial fisheries in the world and serve as essential prey for a number of economically and culturally important species. Thus, there are sufficient data for pollock with which to test ecological theories in an empirical setting. Spatially-explicit predation indices incorporated annual variations in predator biomass, bioenergetics-based rations, and age-specific proportions of pollock consumed by key groundfishes in the Gulf of Alaska (1990 to 2015). We found that Arrowtooth Flounder (*Atheresthes stomias*) was, by far, the dominant pollock predator. We also found synchronous trends in consumption among predator species, indicating a lack of portfolio effects in the region. The combination of a single dominant predator and synchronous predator dynamics suggests strong top-down control over pollock in the Gulf of Alaska. Basin-wide shifts from asynchronous to synchronous consumption suggest diminished trophic stability within the demersal fish community through time. At finer spatial scales (*i.e.,* in the Chirikof and Kodiak statistical

[1] Barnes, CL, Beaudreau AH, Dorn MW, Holsman KK, and Mueter FJ. Accepted. Development of a predation index to assess trophic stability in the Gulf of Alaska. Ecological Applications. Forthcoming.

areas), however, we observed a decrease in synchrony through time. This emphasizes the importance of spatiotemporal heterogeneity in maintaining food web structure and function. Finally, total pollock consumption was highly variable and often exceeded assessment-based estimates of productivity. We assert that using our holistic and empirically-derived predation index as a modifier of assumed constant natural mortality would provide a practical method for incorporating ecological information into single species stock assessments.

1.2 Introduction

Predation has been identified as an important source of mortality for marine fishes, often resulting in far greater losses than those due to fishing (Schoener 1983; Bax 1991; Christensen and Pauly 1993). Although intense predation can have substantial and long-term effects (Polis *et al.* 1996; Link 2002; Hixon and Jones 2005), food webs composed of a wide array of consumers may decrease predator control and promote stability in the population dynamics of prey, when compared to those that are dominated by few predators. The stabilizing effects of diverse predator assemblages are made possible by asynchronous predator dynamics (*e.g.*, trends in abundance, metabolic rates, prey-specific consumption), which lessen overall variability in prey mortality (Polis and Strong 1996; Fu *et al.* 2017; Oken *et al.* 2018). This type of variance reduction is referred to as the 'portfolio effect' (Markowitz 1952; Schindler *et al.* 2015).

Portfolio effects have been used as a way of understanding diversity-stability relationships in a variety of ecological systems (Hooper *et al.* 2005). The basic premise is that community dynamics are less variable than the dynamics of component species by way of statistical averaging (Doak *et al.* 1998). The strength of portfolio effects, therefore, depends upon the degree of covariation among individual species (Tilman 1999). Marginal

or negative covariation tends to decrease overall variance and, thus, increase stability at the community level (McNaughton 1977). Positive covariation, on the other hand, increases the magnitude of community-level variation, thereby decreasing both the potential for portfolio effects and ecosystem stability. The strength of portfolio effects also depends upon the spatial and temporal scale at which observations are made, as variability (*e.g.,* in species abundance or environmental conditions) tends to increase from fine to coarse scales (Levin 1992; Hunsicker *et al.* 2011). From a food web perspective, asynchronous consumption by a diverse assemblage of predators may decrease variability in the predation pressure experienced by prey (Oken *et al.* 2018). Depending upon overall predation intensity, this stabilizing condition may occur at relatively high or relatively low prey abundance.

Considerable shifts in community composition have generated questions about trophic stability in the Gulf of Alaska (Anderson and Piatt 1999; Litzow 2006). What was once a demersal fish community dominated by Walleye Pollock (*Gadus chalcogrammus*; *i.e.*, pollock) – a species that supports some of the world's largest fisheries and serves as important prey for a variety of other stocks (FAO 2014) – is now comprised primarily of upper trophic-level groundfish predators (Anderson and Piatt 1999; Mueter and Norcross 2002). Though this ecological shift has been attributed, at least in part, to warming temperatures (Anderson and Piatt 1999; Bailey 2000), decreases in prey biomass and concurrent increases in predator abundance (*e.g.*, Litzow and Ciannelli 2007; Dorn *et al.* 2017) signify a change in complex predator-prey interactions. Additionally, a number of stock assessment and food web models (*e.g.*, Hollowed *et al.* 2000a; Aydin *et al.* 2007; Gaichas *et al.* 2010; van Kirk *et al.* 2012; Dorn *et al.* 2017) have identified predation mortality as an important driver of pollock biomass within the region. Thus, we were interested in quantifying spatiotemporal variation in predation to better understand the

population dynamics of pollock in the Gulf of Alaska. We also used the concept of the portfolio effect to quantify diversity-stability relationships in a food web context.

We analyzed standardized survey data to quantify spatial and temporal variation in consumption of pollock by major groundfish predators between 1990 and 2015. Time-varying and spatially-explicit indices provide predator-specific and age-structured estimates of predation mortality for pollock. We assert that these predation indices may provide a relatively simple way of integrating ecological information into single species stock assessments (*e.g.,* as a modifier of constant natural mortality, *sensu* Spencer *et al.* 2016). In addition to quantifying predation mortality, we inferred diversity of the predator assemblage by comparing species-specific contributions to overall consumption. We then used consumption estimates to calculate synchrony and portfolio effects as a way of assessing food web stability within the groundfish community. Most studies focusing on portfolio effects have addressed temporal correlations among species, yet asynchrony among locations has been identified as a major contributor to ecosystem stability (Thorson *et al.* 2018). Thus, we calculated synchrony and portfolio effects at four spatial scales: basin, the area encompassed by the stock assessment for Gulf of Alaska pollock (*i.e.*, west of –140° longitude), subregion, and International North Pacific Fisheries Commission (INPFC) statistical area. These spatially-explicit metrics reveal how scale impacts our interpretations of predator diversity, community stability, and the potential for top-down control.

1.3 Methods

1.3.1 Components of the Predation Index

We used stock assessment-based estimates of predator biomass, relative predator densities modeled from fishery-independent surveys (Alaska Fisheries Science Center ([AFSC, National Marine Fisheries Service, National Oceanic and Atmospheric Administration] and the International Pacific Halibut Commission [IPHC]), mean annual rations from bioenergetics models, and food habits data from the AFSC bottom trawl survey to calculate consumption of Walleye Pollock by major groundfishes in the Gulf of Alaska (Fig. 1.1). We calculated time-varying and spatially-explicit indices of predation for young-of-the-year (YOY; 0 yr), juvenile (1 and 2 yr), and adult (3+ yr) pollock (1990 to 2015; Eqn. 1), accounting for five pollock predators – Arrowtooth Flounder (*Atheresthes stomias*), Pacific Cod (*Gadus chalcogrammus*), Pacific Halibut (*Hippoglossus stenolepis*), Sablefish (*Anoplopoma fimbria*), and Walleye Pollock conspecifics. Together, predation by these species is thought to make up over 80% of total mortality for Gulf of Alaska pollock (Gaichas *et al.* 2015; Dorn *et al.* 2017). Species-specific indices of predation were summed across all predators (S) to quantify total consumption of Walleye Pollock (P) at age a in year i and area j as follows:

$$P_{a,i,j} = \sum_{s=1}^{S} P_{s,a,i,j} \text{ , where } P_{s,a,i,j} = B_{s,i} * rD_{s,i,j} * \bar{C}_{s,i,j} * p_{s,i,j} * a_{s,i} \quad (1)$$

$B_{s,i}$ represents total predator biomass (MT converted to g) of predator s in survey year i, as estimated within the most recent stock assessment model for that species. $rD_{s,i,j}$ is the relative density for predator s in year i and area j, which was used to apportion total predator biomass at spatial scales finer than basin-wide. $\bar{C}_{s,i,j}$ denotes mean annual ration (g g^{-1}) for predator s in year i and area j. When multiplied by predator biomass ($B_{s,i} * rD_{s,i,j}$), this component identifies the energetic requirements of each predator species in a given

time and place. $p_{s,i,j}$ denotes the mean proportion of pollock observed in the stomachs of predator s in year i and area j. Multiplying the first four terms of the predation index generates a predator-specific estimate of pollock consumed (g), given predator biomass and mean ration in that particular area and year. Finally, $a_{s,i}$ represents the gravimetric proportion of pollock age class a found in the diets of predator s in year i, allowing for age-specific estimates of pollock consumed. Detailed methods used to estimate each component of the index are described below. We calculated time-varying indices of predation for area j, with the following spatial scales: basin (*i.e.*, entire Gulf of Alaska), subregion (*i.e.*, western, central, eastern Gulf of Alaska), the area encompassed by the stock assessment for Gulf of Alaska pollock (*i.e.*, west of –140° longitude), and statistical area (*i.e.*, Shumagin [610], Chirikof [620], Kodiak [630], Yakutat [640], and Southeastern [650]; Fig. 1.2). All data analyses were conducted using the statistical programming environment R (R Core Team 2018). Data sources and script files can be found at: https://github.com/cheryl-barnes/PollockPredation.git.

1.3.2 Total Predator Biomass, $B_{s,i}$

We compiled estimates of total predator biomass, $B_{s,i}$, from the most recent stock assessment for each species. When combined with other components of the predation index, total predator biomass scales from individual- to population-level consumption. Species-specific $B_{s,i}$ pertain to a subset of each stock (*i.e.*, Arrowtooth Flounder ≥ 19 cm, Pacific Cod ≥ 0 cm, Pacific Halibut ≥ 82 cm, Sablefish ≥ 45 cm, and Walleye Pollock ≥ 37 cm), referred to as 'assessed' fish from here on. Stock assessment estimates of $B_{s,i}$ for Arrowtooth Flounder (Spies *et al.* 2017) and Pacific Cod (Barbeaux *et al.* 2017) encompassed the full extent of the Gulf of Alaska. For Sablefish, we summed subregional

estimates of $B_{s,i}$ (*i.e.,* western Gulf of Alaska, central Gulf of Alaska, west Yakutat, and east Yakutat/Southeast) to account for the entire basin (Hanselman *et al.* 2017). The stock assessment model for Pacific Halibut was developed on a coast-wide scale, combining the Gulf of Alaska, Eastern Bering Sea, Aleutian Islands, British Columbia (Canada), and US West Coast (Stewart and Hicks 2017). Thus, we adjusted $B_{s,i}$ by multiplying coast-wide estimates by the proportion of fish ≥ 32 in (82 cm) caught during IPHC's setline survey (1998 to 2015) in IPHC regulatory areas 4A, 3B, 3A, and 2C. Additionally, the coast-wide assessment did not estimate $B_{s,i}$ for Pacific Halibut prior to 1996. We back-calculated $B_{s,i}$ for 1990 and 1993 based on biomass trends from the AFSC bottom trawl survey (predicted using methods described by Barnes *et al.* 2018), which were highly correlated with those from the IPHC setline survey (Pearson; $r = 0.905$, $t_7 = 5.622$, $p < 0.001$). Walleye Pollock were assessed separately for the areas west and east of $-140°$, referred to as the Gulf of Alaska and Southeast Alaska, respectively (Dorn *et al.* 2017). We summed biomass estimates from the Gulf of Alaska and Southeast Alaska stock assessment models to approximate $B_{s,i}$ for Walleye Pollock at the basin scale. All $B_{s,i}$ estimates were converted to grams before being incorporated into predation indices.

1.3.3 Relative Predator Densities, $rD_{s,i,j}$

We used standardized survey data to estimate relative predators densities throughout the Gulf of Alaska. Bottom trawl survey data collected by the AFSC's Resource Assessment and Conservation Engineering (RACE) Division were used to estimate relative predator densities, $rD_{s,i,j}$, for Arrowtooth Flounder, Pacific Cod, and Walleye Pollock (Fig. 1.2). We used setline and longline survey data to estimate $rD_{s,i,j}$ for Pacific Halibut and Sablefish (Fig. 1.2) because these gear types more effectively sample larger (*i.e.*, older) individuals of

these species. This was an important consideration, given that $B_{s,i}$ obtained from stock assessment models correspond to 8+ yr (≥ 81 cm) Pacific Halibut (Stewart and Hicks 2017) and 2+ yr (≥ 45 cm) Sablefish (Hanselman *et al.* 2017). These size and age ranges are also most likely to consume Walleye Pollock (Yang 1995; Harvey 2009). Additional information about survey designs and data collection methods can be found in Supporting Information.

To improve correspondence between the component of the population used to estimate $rD_{s,i,j}$ and the component estimated by $B_{s,i}$ (*i.e.,* assessed fish), we adjusted haul- or station-specific CPUE (kg per ha) to include only individuals encompassed by stock assessment models (*i.e.*, Arrowtooth Flounder ≥ 19 cm, Pacific Cod ≥ 0 cm, Pacific Halibut ≥ 82 cm, Sablefish ≥ 45 cm, and Walleye Pollock ≥ 37 cm). To adjust CPUE, we first estimated the weight of every fish measured using known length-weight relationships identified in the Arrowtooth Flounder, Pacific Cod, and Sablefish stock assessments (Table S1.1). We used a bias-corrected method described by Brodziak (2012) to quantify the length-weight relationship for Walleye Pollock. We then calculated total mass (*e.g.*, all Arrowtooth Flounder sampled) and mass of assessed individuals (*e.g.*, Arrowtooth Flounder ≥ 19 cm) for each haul or station. The ratio of assessed mass to total mass was then used as a multiplier of haul- or station-specific CPUE. There was no need to calculate weights or adjust CPUE for Pacific Halibut because station-specific estimates of ≥ 32 in (82 cm) were provided.

We used delta (*i.e.*, hurdle) models to quantify species-specific probability of occurrence and log-transformed CPUE for positive catches (*sensu* Barnes *et al.* 2018). Presence-absence and log-transformed CPUE were modeled as a function of survey year, location (latitude and longitude), and depth. Bottom temperatures were available from trawl surveys and included as an additional covariate for Arrowtooth Flounder, Pacific Cod, and Walleye

Pollock models. Temperature data were only available during the latter portions of the IPHC setline and AFSC longline surveys. Thus, temperature was excluded from models pertaining to Pacific Halibut and Sablefish. For computational efficiency, we generated a comprehensive suite of alternative generalized additive models (GAMs; 'mgcv' package, Wood 2011; 'MuMIn' package, Bartoń 2017) and used ΔAIC to identify best-fit GAMs. We then re-ran best-fit GAMs as generalized additive mixed models (GAMMs) with and without a Gaussian spatial autocorrelation structure that varied by survey year ('mgcv' package, Wood 2011). Only GAMMs with spatial autocorrelation that resulted in an improved fit were selected over best-fit GAMs.

Final models were used to quantify probabilities of occurrence PO and predicted abundances PA across a 50 km by 50 km uniform grid spanning the study area. We multiplied the $PO_{s_{i,g}}$ and $PA_{s_{i,g}}$ for species s in year i and grid cell g to estimate predator density $D_{s,i,g}$. We then calculated relative predator densities $rD_{s,i,g}$ by dividing $D_{s,i,g}$ by the sum of all grid cells sampled in year i ($rD_{s,i,g} = \frac{D_{s,i,g}}{\sum_{g=1}^{G} D_{s,i,g}}$, where G is the total number of grid cells g sampled in year i). Thus, the sum of $rD_{s,i,g}$ across all grid cells was equal to one in a given year, representing the basin scale. We summed $rD_{s,i,g}$ within each statistical area to quantify $rD_{s,i,j}$ at intermediate spatial scales. For the subregion scale, we recategorized the Shumagin statistical area (610) as the western Gulf of Alaska, summed $rD_{s,i,g}$ estimates within the Chirikof (620) and Kodiak (630) statistical areas to represent the central subregion, and summed $rD_{s,i,g}$ in the Yakutat (640) and Southeastern (650) statistical areas as the eastern subregion. These subregions are consistent with definitions used by the AFSC (*e.g.,* Aydin *et al.* 2007; Dorn *et al.* 2017). Finally, we summed $rD_{s,i,g}$ within the area encompassed by the stock assessment for Gulf of Alaska pollock (*i.e.*, the area west of –

140° longitude). There were no IPHC setline survey data prior to 1998. Thus, we assigned area-specific mean densities for Pacific Halibut using the available time series (1998 to 2017) in 1990, 1993, and 1996. When multiplied by $B_{s,i}$, $rD_{s,i,j}$ provides an estimate of predator biomass in each year and area of interest.

1.3.4 Mean Annual Rations, $\bar{C}_{s,i,j}$

We used Wisconsin bioenergetics models (Kitchell *et al.* 1977; Deslauriers *et al.* 2017) to calculate maximum daily consumption rates, C_{max} (g g^{-1} d^{-1}) for assessed fish. C_{max} was estimated as a function of individual predator weight W and haul-specific temperature T_h (Hanson *et al.* 1997; Holsman and Aydin 2015) such that:

$$C_{max} = C_A * W^{C_B} * f(T_h), \text{ where} \quad (2)$$

$$f(T_h) = V^X * e^{X(1-V)},$$

$$V = \frac{T_{C_M} - T_h}{T_{C_M} - T_{C_0}}, \quad X = \frac{Z^2 * (1 + \left(1 + \frac{40}{Y}\right)^{0.5})^2}{400}, \text{ and}$$

$$Z = \log(C_Q) * (T_{C_M} - T_{C_0}), \quad Y = log(C_Q) * (T_{C_M} - T_{C_0} + 2)$$

C_A and C_B are the intercept and slope for the allometric consumption equation based on predator weight (kg), and are scaled by temperature $f(T_h)$. T_{C_M} represents the temperature threshold above which consumption ceases, T_{C_0} is the temperature where consumption rates are greatest, and C_Q approximates the rate of increase in consumption at low temperatures. Bioenergetics model parameters were sourced from Holsman and Aydin (2015), Holsman *et al.* (2019), Holsman *et al.* (unpubl. data), and Harvey (2009) (Table 1.1). Individual weights were only measured for predators that were subsampled for food habits data as part of the AFSC bottom trawl survey. Thus, we relied on this subset of assessed fish to estimate maximum daily consumption for each of our focal predators. Temperature

data were missing in the Shumagin statistical area in 1990, so C_{max} estimates were assumed to be the same as those in Shumagin in 1993. After 2011, we also assumed mean C_{max} for Sablefish within each statistical area because this species was not sampled for food habits information in 2013 or 2015. We then multiplied C_{max} by the estimated number of foraging days per predator per year to scale from maximum daily consumption (C_{max}, g g^{-1} d^{-1}) to maximum annual consumption, C_{max} (g g^{-1} yr^{-1}) (Table 1.1; Holsman and Aydin 2015; Holsman *et al.*, unpubl. data; Holsman *et al.* 2019). We averaged mass- and temperature-specific annual rations for species s in year i and area j ($\bar{C}_{s,i,j}$) for inclusion in predation indices. Multiplying $B_{s,i}$, $rD_{s,i,j}$, and $\bar{C}_{s,i,j}$ estimates the year- and area-specific energetic requirements of each predator species.

1.3.5 Proportions of Pollock Consumed, $p_{s,i,j}$

We used food habits data collected by the AFSC's Resource Ecology and Ecosystem Modeling (REEM) Program to quantify proportions of pollock in the diets of assessed fish. Food habits data were unavailable from the IPHC setline and AFSC longline surveys due to high rates of regurgitation that result from prolonged fishing (Stewart pers. comm. 14 Feb 2018). Therefore, dietary analyses were based on data from the AFSC bottom trawl survey. Subsampling methods and additional information about food habits data collection can be found in Supporting Information.

As a result of size-structured subsampling, fork lengths of fish selected for stomach content analyses were not representative of the overall catch. To correct for this, we weighted food habits data according to size-specific proportions of predators sampled. First, we defined 10-cm fork length bins b for each predator species s. We then calculated proportions of assessed fish caught in each length bin b and haul h. This was done for each

species s using a) all fish caught during the bottom trawl survey ($P_{T_{s,b,i,h}} = \frac{N_{T_{s,b,i,h}}}{\sum_{h=1}^{H} N_{T_{s,i,h}}}$) and b) only fish subsampled for food habits ($P_{F_{s,b,i,h}} = \frac{N_{F_{s,b,i,h}}}{\sum_{h=1}^{H} N_{F_{s,i,h}}}$). N denotes the total number of fish sampled and H represents the total number of hauls conducted. Weighting factors, WF_L, were calculated by dividing size-specific proportions of assessed (*i.e.,* 'total') fish, P_T, , in year i and haul h by proportions of fish subsampled for food habits, P_F, within the same sampling group: $WF_{L_{s,b,i,h}} = \frac{P_{T_{s,b,i,h}}}{P_{F_{s,b,i,h}}}$.

In addition to size-structured subsampling, survey effort was not proportional to predator biomass. Thus, biomass weighting was necessary to scale up from individual predator diets. Biomass weighting factors, WF_B, were calculated by dividing predicted densities for species s in year i and grid cell g ($D_{s,i,g}$; described above) by the mean predicted density in year i ($\overline{D}_{s,i}$): $WF_{B_{s,i,g}} = \frac{D_{s,i,g}}{\overline{D}_{s,i}}$. We then weighted raw food habits data by multiplying the mass of each prey taxa q observed in individual predator stomach r ($w_{q,r}$) by fork length and biomass weighting factors ($w_{w_{q,r}} = w_{q,r} * WF_L * WF_B$). Species s, year i, and location (haul h or grid cell g) subscripts were removed for simplicity. Finally, we used fork length- and biomass-weighted food habits data to estimate proportions of prey consumed, p_q, by predator species s in year i and area j as follows:

$$p_q = \frac{\sum_{r=1}^{R} w_{w_{q,r}}}{\sum_{r=1}^{R}\sum_{q=1}^{Q} w_{w_{q,r}}}, \text{ where} \quad (3)$$

Q represents the total number of prey taxa and R is the total number of predator stomachs observed (Chipps and Garvey 2007). Proportions of pollock, termed $p_{s,i,j}$, were included in predation indices. We assumed mean $p_{s,j}$ for Sablefish in 2013 and 2015, when no diet data were collected.

1.3.6 Age Compositions of Pollock as Prey, $a_{s,i}$

The stock assessment for Gulf of Alaska pollock accounts for age-specific mortality (Dorn *et al.* 2017). Thus, we were interested in quantifying age-specific predation mortality for pollock. First, we used all available bottom trawl survey data to quantify age-length (von Bertalanffy 1938) and bias-corrected length-weight (Brodziak 2012) relationships for pollock in the Gulf of Alaska. We then used parameters from these relationships to estimate ages and weights of pollock found in the stomachs of each predator. Due to variable stages of digestion, only a subset of pollock found were measurable (standard length, mm) from stomach contents. From these, we used multinomial logistic GAMs ('VGAM' package in R, Yee 2015) to estimate mean proportions of age-0, age-1, age-2, and age-3+ pollock consumed by species s in year i ($a_{s,i}$). Small sample sizes precluded spatially-explicit analyses of pollock age. Measurable pollock were not observed in the diets of Sablefish in 2005, 2013, and 2015 or Walleye Pollock in 2005, 2011, and 2015. For these species and years, we assigned mean a_s across all years.

1.3.7 Predation Indices, $P_{a,i,j}$, and Variance Ratios

We calculated age-specific consumption of Walleye Pollock by predator species, year, and area ($P_{a,s,i,j}$, Eqn. 1) at the following spatial scales: basin, the area encompassed by the stock assessment for Gulf of Alaska pollock, subregion, and statistical area. We summed predator-specific indices to estimate 'total' predation on pollock through time. Data limitations precluded estimates in the eastern Gulf of Alaska between 1996 and 2001, in the Yakutat statistical area from 1996 to 2001, and in the Southeastern statistical area prior to 2005. We calculated relative predator contributions to pollock predation mortality by dividing $P_{a,s,i,j}$ by $P_{a,i,j}$. Finally, we calculated variance ratios – a measure of correlation among

multivariate responses – to assess the degree of synchrony in pollock consumption among predators (Loreau and de Mazancourt 2008; Gonzalez and Loreau 2009; Oken *et al.* 2018). Variance ratios, VR_j, were computed as follows: $VR_j = \frac{var[P_j]}{\sum var[P_{s,j}]}$, where $var[P_j]$ represents variance for total pollock consumption (all predators combined) in area j across all years and $\sum var[P_{s,j}]$ is the sum of variances for predator-specific consumption in area j across all years. VR_j is equal to one when consumption is, on average, statistically independent among predators (*i.e.*, overall variance is equivalent to the sum of predator-specific variances). A VR_j greater than one suggests synchronous trends in consumption among species (*i.e.*, the sum of predator-specific variances is less than the variance of total consumption) and a VR_j less than one indicates asynchrony (*i.e.*, the sum of predator-specific variances is greater than the variance of total consumption).

The degree of portfolio effect PE_j was estimated as 1 - VR_j (*e.g.,* Thorson *et al.* 2018). We then used PE_j to make inferences about stability in the predation pressure experienced by Walleye Pollock, with higher PE_j reflecting greater trophic stability and lower PE_j suggesting more unstable food web interactions in a particular area and time period. Due to data limitations, we were only able to calculate VR_j and PE_j for the eastern Gulf of Alaska during the latter portion of the time series (*i.e.*, 2005 onward). Thus, we analyzed the early portion (1990 to 2003) and the full (1990 to 2015) time series to compare VR_j and PE_j for the western and central subregions (*i.e.*, Shumagin, Chirikof, and Kodiak statistical areas). We separately computed VR_j and PE_j for the latter half of the time series to assess temporal changes in synchrony, portfolio effects, and trophic stability across all subregions and statistical areas. We calculated Pearson's correlation matrices to quantity species-specific correlations in pollock consumption at each spatial scale. We also explored

spatiotemporal anomalies in consumption by dividing species-, subregion- and year-specific consumption by the species-specific means for the entire Gulf of Alaska and time series. To understand how predation mortality compared to estimates of pollock productivity, we calculated year-specific ratios of age-3+ consumption to total pollock biomass within the area encompassed by the stock assessment (Dorn *et al.* 2017).

1.4 Results

1.4.1 Components of the Predation Index

Arrowtooth Flounder biomass ($B_{s,i}$) increased from 1990 to 2005 and decreased between 2007 and 2015 (Table 1.2). Walleye Pollock showed the opposite trend, though with greater interannual variability. Pacific Cod and Pacific Halibut exhibited overall declines in $B_{s,i}$ throughout the time series and there was no clear trend in Sablefish $B_{s,i}$.

When estimating $rD_{s,i,j}$, we found that full models best described the distributions and abundances of each species (Tables S1.2 and S1.3; Figs. S1.1 and S1.2). Accounting for spatial autocorrelation improved the fit for all models except those pertaining to Walleye Pollock (Table S1.4). GAMMs did not converge for modeling presence-absence of Pacific Halibut. Because Sablefish were observed at nearly all stations encompassed within the AFSC longline survey, we did not separately model presence-absence for this species. Arrowtooth Flounder, Pacific Cod, and Walleye Pollock $rD_{s,i,j}$ were highest in the western and central subregions, whereas $rD_{s,i,j}$ for Pacific Halibut and Sablefish were more evenly distributed throughout the study area (Fig. 1.3).

Sablefish had the highest consumption rates of all predators examined ($\bar{C}_{s,i,j}$; 5.7 $\pm$ 0.32 SD), followed by Pacific Halibut (4.9 $\pm$ 0.36 SD) (Fig. 1.4). $\bar{C}_{s,i,j}$ for Arrowtooth Flounder and Pacific Cod were similar to one another (3.7 $\pm$ 0.28 SD and 3.7 $\pm$ 0.27 SD), and Walleye

Pollock had the lowest $\bar{C}_{s,i,j}$ of any species (1.5 $\pm$ 0.09 SD). Despite differences in relative estimates, all predators displayed similar trends in mean annual ration through time, including a peak in $\bar{C}_{s,i,j}$ in 2003 and relatively little variation throughout the remainder of the time series.

Diet compositions (Fig. S1.3) showed the greatest proportions of pollock ($p_{s,i,j}$) for Arrowtooth Flounder (0.45 $\pm$ 0.20 SD) and Pacific Halibut (0.33 $\pm$ 0.16 SD) (Fig. 1.4). Pacific Cod and Sablefish consumed proportionally less pollock (0.17 $\pm$ 0.16 SD and 0.14 $\pm$ 0.13 SD), and Walleye Pollock had relatively few conspecifics (0.04 $\pm$ 0.06 SD) in their diets (Fig. 1.4). Pollock observed in Arrowtooth Flounder stomachs were a mixture of adult and juvenile fish (age-3+: 0.38 $\pm$ 0.09 SD, age-2: 0.26 $\pm$ 0.11 SD, age-1: 0.30 $\pm$ 0.12), whereas Pacific Halibut fed primarily on adult pollock (age-3+: 0.84 $\pm$ 0.04 SD). Adults made up the greatest proportion of pollock consumed by Pacific Cod (0.58 $\pm$ 0.21 SD) and juveniles were more common in Sablefish diets (0.74 $\pm$ 0.20 SD). Cannibalized pollock were either age-0 (0.62 $\pm$ 0.23 SD) or age-1 (0.38 $\pm$ 0.23 SD) fish.

1.4.2 Predation Indices, $P_{a,i,j}$, and Variance Ratios

$P_{a,i,j}$ ranged from 1.81 to 7.61 million MT in the Gulf of Alaska. Arrowtooth Flounder were responsible for the vast majority of predation, followed by Pacific Halibut, Pacific Cod, Sablefish, and Walleye Pollock (Table 1.3). Most pollock prey by weight were age-3+ adults (0.431 $\pm$ 0.045 SD), followed by age-1 (0.257 $\pm$ 0.080 SD) and age-2 (0.240 $\pm$ 0.086 SD) juveniles (Fig. 1.4). Relatively few (0.070 $\pm$ 0.023 SD) young-of-the-year pollock were observed overall. $P_{a,i,j}$ was greatest in 1996 and 2003, with subsequent peaks in 2007 and 2013 (Fig. 1.5). Each peak was followed by a considerable decrease in $P_{a,i,j}$ that coincided with decreases in proportions of pollock consumed by Arrowtooth Flounder ($p_{s,i,j}$; Fig. 1.4).

Spatiotemporal anomalies in total pollock predation closely resembled consumption by Arrowtooth Flounder (Fig. 1.6). We found the greatest consumption of pollock in the central Gulf of Alaska, which was approximately evenly distributed between the Chirikof and Kodiak statistical areas (Fig. 1.7). There was a general decline in $P_{a,i,j}$ throughout the time series. There was no correlation between pollock biomass and age-3+ consumption prior to 2005 (r_4 = 0.372, p = 0.468), but a negative correlation thereafter (r_4 = -0.823, p = 0.044). Additionally, we found that consumption of age-3+ pollock exceeded stock assessment-based estimates of total biomass between 1996 and 2007 (Fig. 1.8; Dorn *et al.* 2017). Consumption ($P_{a,i,j}$) to biomass ($B_{s,i}$) ratios ranged from 0.45 in 2015 to 3.57 in 2001. $P_{a,i,j}$ was less than pollock $B_{s,i}$ from 2009 to 2015.

Variance ratios pertaining to the full time series indicated synchronous trends in consumption among predators ($VR_j > 1$) and, thus, a lack of portfolio effects at all spatial scales (Table 1.4). Pollock consumption was most synchronous at the basin scale. All other locations and spatial scales showed slightly less, but similar degrees of synchrony. We found a positive correlation between pollock consumption by Arrowtooth Flounder and Sablefish in the Kodiak statistical area and a negative correlation between consumption by Arrowtooth Flounder and Pacific Halibut in the Southeastern statistical area (Table 1.5). There were no other correlations between Arrowtooth Flounder and other predators at any other spatial scale. Positive correlations were common among predator species other than Arrowtooth Flounder, except in the Shumagin (*i.e.*, western subregion) or Yakutat statistical areas, where no correlations were detected.

We found a variety of temporal shifts in synchrony and portfolio effects when separately quantifying variance ratios for 'early' (1990 to 2003) and 'late' (2005 to 2015) portions of the time series. At the basin scale, species-specific trends in pollock consumption shifted from

asynchronous (VR_j < 1) to synchronous (VR_j > 1). Predation within the pollock assessment area was also asynchronous during the earlier time period, and became more independent ($VR_j \approx 1$) in later years. Similar to the basin-scale, pollock consumption in the western subregion shifted from asynchronous to synchronous between the two time periods. Conversely, the degree of synchrony decreased over time in the central Gulf of Alaska (Table 1.4). The eastern subregion displayed uncorrelated trends in pollock predation, with the greatest degree of asynchrony in the Southeastern statistical area.

1.5 Discussion

We found Arrowtooth Flounder to be the dominant pollock predator in the Gulf of Alaska, regardless of spatial scale or time period. Though the remaining groundfish predators consumed much less pollock, trends in consumption were synchronous among them. The combination of a single dominant predator and synchronous consumption dynamics suggests potential for strong top-down control over pollock in the Gulf of Alaska. This is because a diverse predator assemblage is likely to generate stabilizing effects (*i.e.,* relatively constant predation pressure through asynchronous consumption dynamics) in time and space, thereby decreasing the effect strength of any one predator (Power 1992; Polis and Strong 1996; Oken *et al.* 2018). Basin-wide shifts from asynchronous to synchronous consumption dynamics also suggest diminished trophic stability for the demersal fish community through time. However, finer spatial scales (*e.g.*, different subregions and statistical areas) generated variable estimates of synchrony, reflecting substantial spatial heterogeneity throughout the region. Although the western subregion shifted to more synchronous pollock consumption through time, an increased portfolio effect in the central subregion may help buffer against greater trophic instability at the basin scale,

thus aiding in the maintainence of food web structure and function in the Gulf of Alaska. We were unable to assess temporal trends in synchrony and stability in the eastern Gulf of Alaska, which showed some evidence for portfolio effects during the late time period.

1.5.1 Variation in Predation Intensity

Although Walleye Pollock represents an important prey source for many economically important species, consumption was not uniformly distributed among groundfishes in the Gulf of Alaska. Arrowtooth Flounder was the dominant pollock predator, representing 74% of total consumption among the five species examined. Food web models parameterized using the same bottom trawl survey and food habits data between 1990 and 1996 estimated that 54.5% of pollock predation mortality (juveniles and adults combined) was due to consumption by Arrowtooth Flounder (Aydin *et al.* 2007; Gaichas *et al.* 2010). Remaining predation mortality (among our target groundfish predators) was 12.1% from Pacific Cod, 15.4% from Pacific Halibut, 4.2% from Sablefish, and 13.8% from Walleye Pollock. We attribute overall differences in relative predator contributions to the inclusion of bottom trawl survey and diet data between 1999 and 2015. When we restricted predation indices to the first few years of the time series (*i.e.,* 1990, 1993, and 1996 – largely the same dataset used in regional food web models), our predator-specific contributions to pollock mortality were more similar to previous studies (*i.e.*, 59% Arrowtooth Flounder, 25% Pacific Halibut, 8% Pacific Cod, 6% Sablefish, and 2% Walleye Pollock). This is because analyses that extend beyond 1996 include a time period (~ 2005 to 2011) when pollock consumption was negligible for Pacific Cod, Pacific Halibut, Sablefish, and Walleye Pollock, compared to Arrowtooth Flounder. However, absolute predation intensity was much greater in this study. For example, Hollowed *et al.* (2000a) estimated pollock consumption by Arrowtooth Flounder to be 3.0×10^5 MT in 1997. Another study by van Kirk *et al.* (2010) estimated

consumption by Arrowtooth Flounder to be 1.7 x 10^5 MT that same year. Our estimate of pollock consumed by Arrowtooth Flounder for 1997 (a mean of consumption from 1996 and 1999) was considerably higher, at 3.8 x 10^6 MT. As such, we recommend that predation indices be used to track relative changes in predation intensity rather than infer absolute removals by groundfish predators.

Food web models have indicated periods when predation mortality exceeded assessment-based estimates of production (Dorn *et al.* 2017), corroborating the relatively high estimates from our study. However, there are several potential reasons why our estimates of predation intensity differed from those provided by other authors. First, our values for $\bar{C}_{s,i,j}$ were likely biased high because they were calculated from bioenergetics models that assumed predators fed at their theoretical maximum consumption rates (C_{max} = 1). Most fishes feed at rates less than half their theoretical maximum (*i.e.*, median proportion of C_{max} = 0.43 across 66 populations from 38 species; Armstrong and Schindler 2011). Relative foraging rates are available for all of our focal species (Table S1.5; Harvey 2009; Holsman and Aydin 2015) and could be used to modify C_{max} when calculating $\bar{C}_{s,i,j}$ (*sensu* Holsman and Aydin 2015; Spencer *et al.* 2016). Additionally, we calculated C_{max} using bottom temperatures from summer surveys. Effective foraging days, which make use of the von Bertalanffy growth function to integrate physical and trophodynamics processes over the course of a year, allowed for scaling from daily consumption to annual rations (Holsman and Aydin 2015). However, we did not directly account for cooler temperatures (and thus, decreased metabolic rates) in fall, winter, or spring. We also relied upon empirical data from European Plaice (*Pleuronectes platessa;* Fonds *et al.* 1992) to estimate bioenergetics parameters for Arrowtooth Flounder (Holsman and Aydin 2015). This is because laboratory experiments aimed at parameterizing allometric consumption and

temperature scaling functions for Arrowtooth Flounder have been unsuccessful due to a lack of foraging in captivity (Holsman pers. obs). Because Arrowtooth Flounder was identified as the dominant pollock predator, species-specific bioenergetics parameters would improve predation indices as well as contribute to our understanding about food web stability in the Gulf of Alaska.

Another methodological difference that can explain divergence between our results and prior estimates of pollock predation is that we weighted diet data to correct for biases in subsampling stomachs during the bottom trawl survey following Livingston *et al.* (2017). Fork length- and biomass-weighting is not consistently incorporated into dietary analyses for groundfish predators in the Gulf of Alaska. Aydin *et al.* (2007) and Gaichas *et al.* (2010) biomass-weighted food habits data to account for spatial differences in their multispecies models. Given that diet data resulted from a size-structured sampling design, weighting by predator fork length is also necessary to scale to population levels (Livingston *et al.* 2017). In most cases, we found that weighting diet data by fork length did not drastically alter $p_{s,i,j}$ (Fig. S1.3). Notably, however, our predation indices were sensitive to proportional diet data, with small variations being magnified by other components (*e.g.,* $B_{s,i}$). Finally, our predation index was designed to represent consumption by assessed groundfish predators (*i.e.,* those included in estimates of total biomass: Arrowtooth Flounder $\geq$ 19 cm, Pacific Cod $\geq$ 0 cm, Pacific Halibut $\geq$ 82 cm, Sablefish $\geq$ 45 cm, and Walleye Pollock $\geq$ 37 cm). Thus, we emphasized the size classes most likely to consume pollock. Including other predators (*e.g.,* Steller Sea Lions) and smaller size classes of one or more focal species would increase absolute estimates of pollock predation; however spatiotemporal trends presented here should be robust all major sources of pollock predation were represented (Dorn *et al.* 2017).

1.5.2 Predator Dominance, Portfolio Effects, and Trophic Stability

Arrowtooth Flounder comprise the greatest biomass of any tertiary consumer in the Gulf of Alaska (Spies *et al.* 2017). They also maintain an extensive network of food web connections (Gaichas and Francis 2008). As a result, regional ecosystem models indicate that minor changes in Arrowtooth Flounder abundance can have considerable impacts on a variety of interacting species (Aydin *et al.* 2007). We found that Arrowtooth Flounder biomass ($B_{s,i}$) and relative contributions to pollock predation ($P_{a,i,j}$) followed the same general trends, increasing from 1993 to 2007 and decreasing thereafter. Trends in pollock biomass ($B_{s,i}$) contrasted those for Arrowtooth Flounder. Though a recent multispecies spatial model found a small negative correlation between Arrowtooth Flounder and Walleye Pollock in the Gulf of Alaska (Thorson *et al.* accepted), these opposite trajectories – along with a predator assemblage that is dominated by one species – support the hypothesis that Arrowtooth Flounder exert top-down control over Gulf of Alaska pollock (Hollowed *et al.* 2000a; Aydin *et al.* 2007; Gaichas *et al.* 2010; van Kirk *et al.* 2010; Holsman *et al.* 2016). Oken *et al.* (2018) reached a similar conclusion regarding substantial predatory effects of Arrowtooth Flounder on Pacific Herring (*Clupea pallasii*), demonstrating that their predatory influence is not limited to pollock in the region.

Asynchronous consumption trends among species or locations may generate portfolio effects that help buffer against strong predatory control (McNaughton 1977; Hooper *et al.* 2005; Schindler *et al.* 2015). Using the full time series, we found only synchronous trends in pollock consumption. This points toward a lack of portfolio effects and the potential for trophic instability among Gulf of Alaska groundfishes. We also found increased synchrony between early and late time periods at the basin scale, indicating decreased stability through time. This finding corroborates those in a previous study, which indicated low

predictability and high potential for predatory control in the 'top heavy' Gulf of Alaska food web (Gaichas *et al.* 2015). Despite this, the central subregion, which comprised the greatest proportion of pollock consumption overall, showed decreased synchrony from early to late time periods. This suggests that trophic interactions among groundfish species are becoming more stable in the central Gulf of Alaska, despite frequent and substantial changes in predation intensity over time. Asynchronous consumption was also evident in Chirikof and Southeastern statistical areas when analyzed separately, demonstrating the positive effects of spatial heterogeneity on community stability (Schindler *et al.* 2010). In fact, spatial asynchrony can generate greater portfolio effects than asynchronous trends among species (Thorson *et al.* 2018). This is an important consideration in the context of diversity-stability relationships in systems comprised of few dominant predators (*e.g.,* Baltic Sea sprat, Eastern Scotian forage fishes, and Pacific Herring in the Gulf of Alaska; Oken *et al.* 2018). For example, more stable predator-prey interactions in the Chirikof and Southeastern statistical areas may provide a buffer for highly variable predation intensity in the western Gulf of Alaska.

Positive portfolio effects and greater trophic stability in the central and eastern subregions during the later time period are plausible given recent decreases in Arrowtooth Flounder biomass (Spies *et al.* 2017). A longer time series of survey data would permit multi-year moving window estimates of portfolio effects (*e.g.,* Thorson *et al.* 2018), which would aid in the identification of bottom-up and top-down mechanisms for changing trophic stability in the Gulf of Alaska. Additionally, modeling predation intensity as a function of key environmental variables (*sensu* Litzow and Ciannelli 2007) would contribute to our understanding about reorganization within the demersal fish community and changes in trophic stability related to rapid climate change.

1.5.3 Implications for Fisheries Management

We found that $P_{a,i,j}$ exceeded $B_{s,i}$ in over half of the study period. There was also substantial variation in $P_{a,i,j}$ within the area encompassed by the stock assessment for Gulf of Alaska pollock. High consumption to biomass ratios, combined with considerable variation in consumption through time, reiterate the need to account for temporal changes in predation mortality when assessing Gulf of Alaska pollock. Regional differences in predation intensity and community stability also suggest that a spatially-explicit approach (*e.g.,* Spencer *et al.* 2016) may be warranted. A plethora of case studies (*e.g.*, Magnusson 1995; Gislason 1999; Hollowed *et al.* 2000b; Jurado-Molina *et al.* 2005; Moustahfid *et al.* 2009; van Kirk *et al.* 2010; Tyrrell *et al.* 2011; Holsman *et al.* 2016) have shown that including ecological parameters such as predation intensity directly into stock assessments can alter the magnitude and uncertainty of biological reference points, and generally leads to more conservative harvest limits. To date, methods for quantifying pollock predation mortality in the Gulf of Alaska have relied on highly complex multispecies models. A simpler approach to operationalizing ecosystem-based fisheries management would be to use changes in predation intensity as a modifier of constant natural mortality (*e.g.*, Hollowed *et al.* 2000a; Livingston and Methot 1998; A'mar *et al.* 2010; Spencer *et al.* 2016). We assert that our empirically-derived, time-varying, spatially-explicit, and age-structured predation index is well suited to account for complex ecological processes in this way. Estimates of predation mortality can also be included as part of an ecosystem and socioeconomic profile (ESP) – a standardized appendix to the stock assessment that provides relevant information on ecosystem and socioeconomic aspects of important stocks (*e.g.,* Shotwell *et al.* 2019). Though our results are most applicable to the species, areas, and time periods included in

this case study, our analytical approach can be used to estimate predation mortality, trophic stability, and the degree of top-down control in large marine ecosystems around the world.

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1.8 Figures

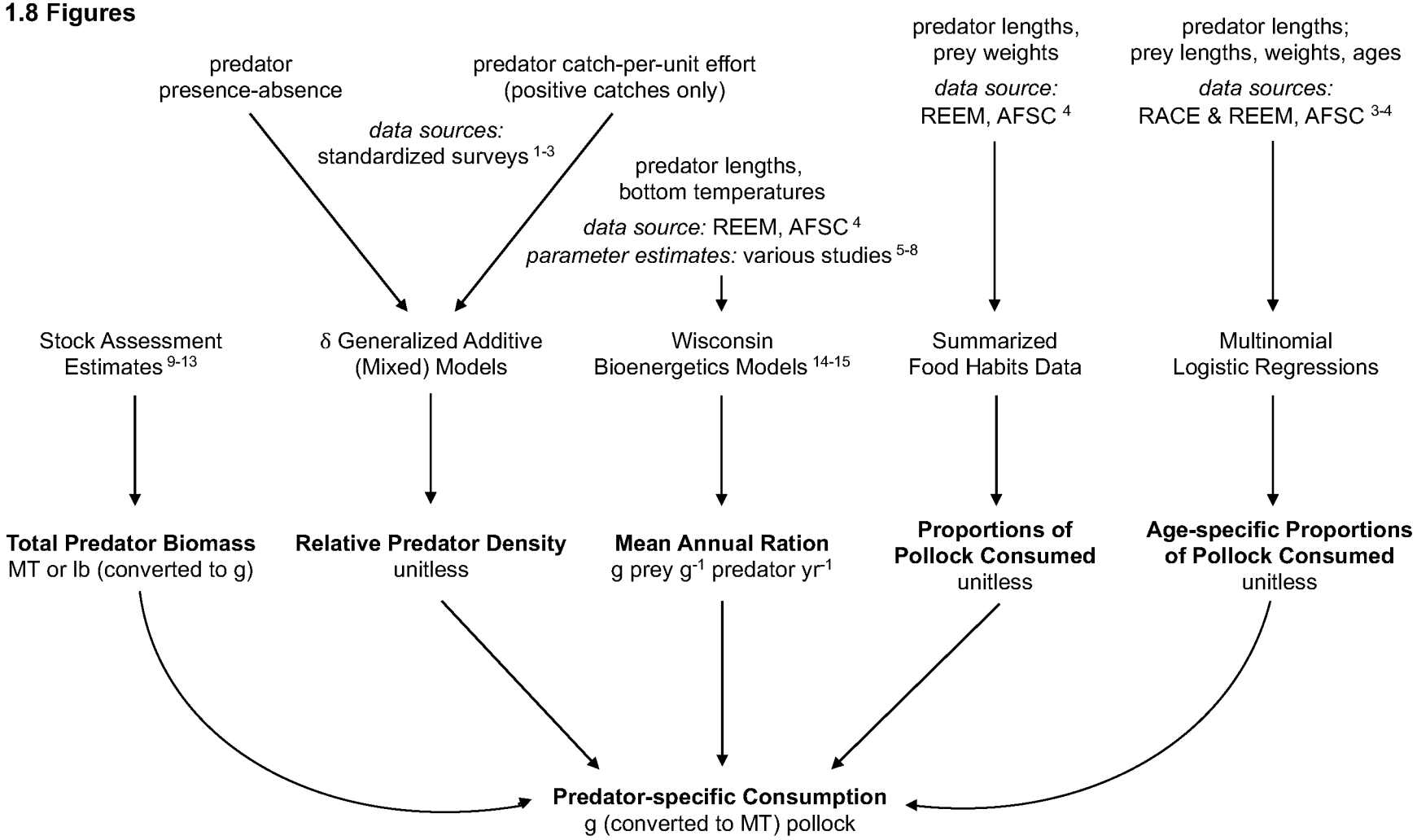

Figure 1.1 Conceptual diagram of workflow (data sources and analytical methods) used to estimate predator-, year-, and area-specific consumption of Walleye Pollock in the Gulf of Alaska (1990 to 2015). References: [1] Sigler and Lunsford (accessed 2019), [2] Soderlund *et al.* 2012; [3] von Szalay *et al.* 2016, [4] Livingston *et al.* 2017, [5] Harvey 2009, [6] Holsman and Aydin 2015, [7] Holsman *et al.* 2019, [8] Holsman *et al.* (unpubl. data), [9] Barbeaux *et al.* 2017; [10] Dorn *et al.* 2017, [11] Hanselman *et al.* 2017, [12] Spies *et al.* 2017, [13] Stewart and Hicks 2017, [14] Kitchell *et al.* 1997, [15] Deslauriers *et al.* 2017.

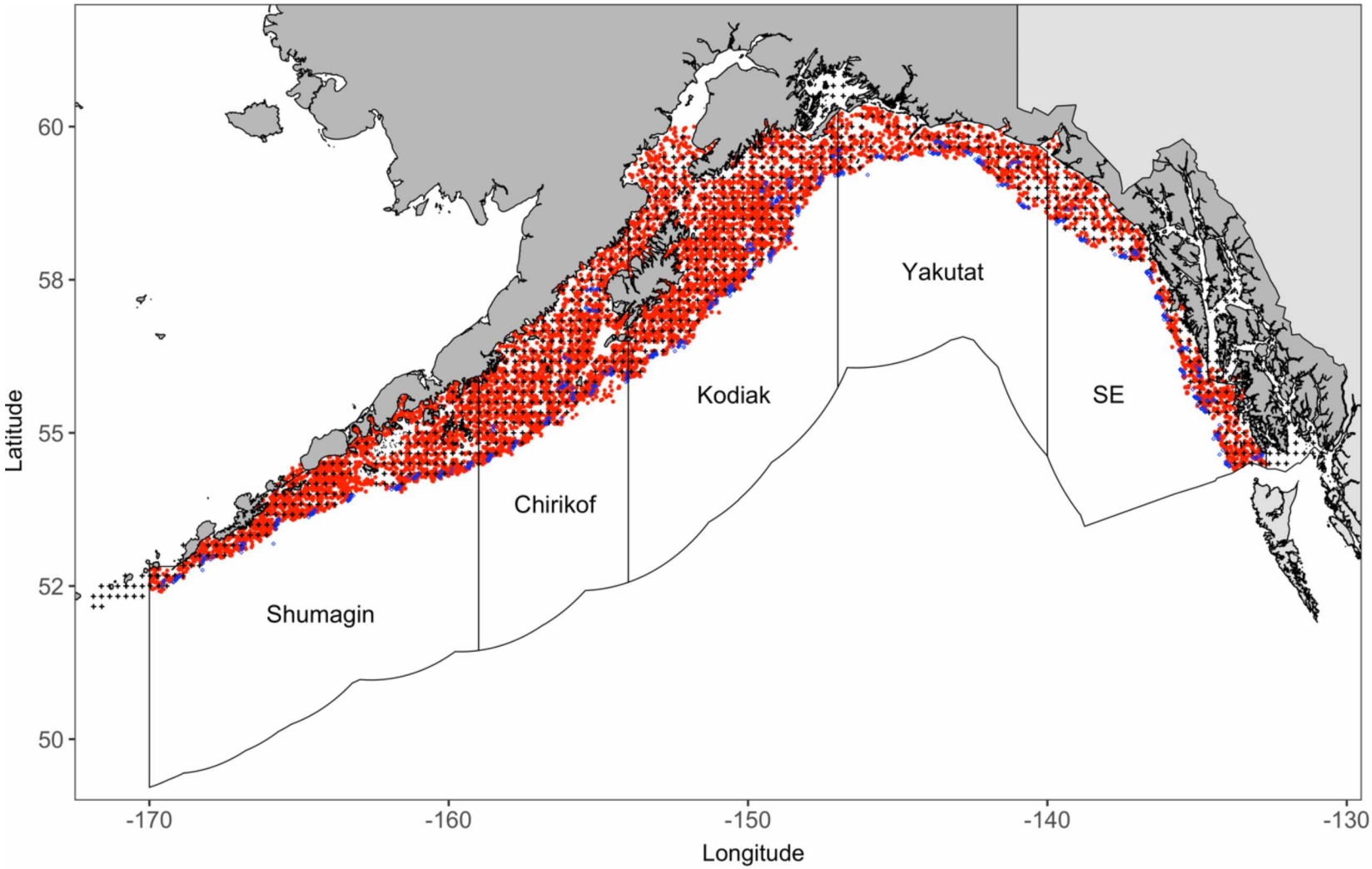

Figure 1.2 Map of study area (Gulf of Alaska, 1990 to 2015). Red dots indicate tow locations of the Alaska Fisheries Science Center (AFSC) bottom trawl survey, black crosses indicate International Pacific Halibut Commission (IPHC) setline survey stations, and blue dots denote AFSC longline survey stations. Unfilled polygons outlined in black denote Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern (SE) statistical areas defined by the International North Pacific Fisheries Commission (INPFC).

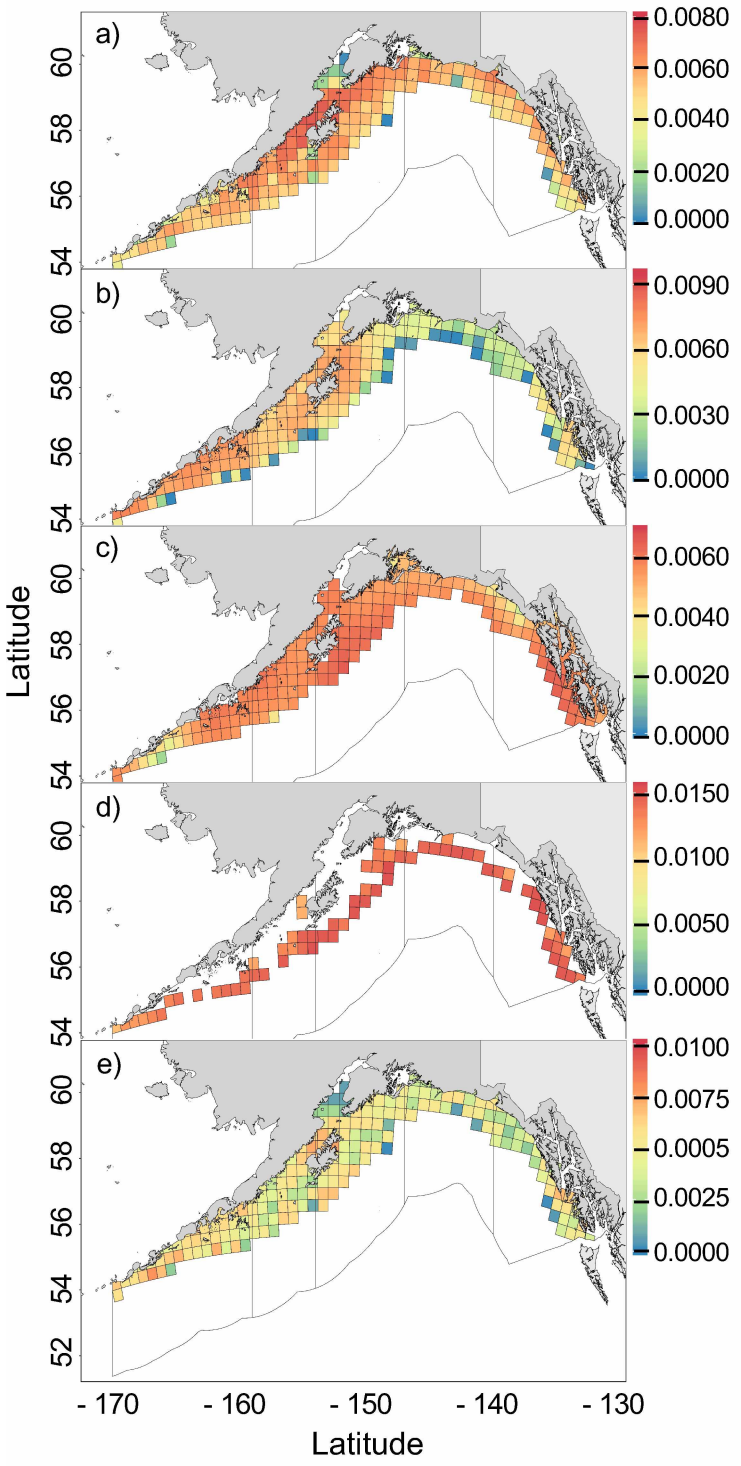

Figure 1.3 Relative predator densities $rD_{s,i,j}$ for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock, Gulf of Alaska (1990 to 2015). Warm colors show higher densities and cool colors show lower densities. Squares represent 50 km by 50 km grid cells. Polygons indicate statistical areas defined by the International North Pacific Fisheries Commission (INPFC). West to east: Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern.

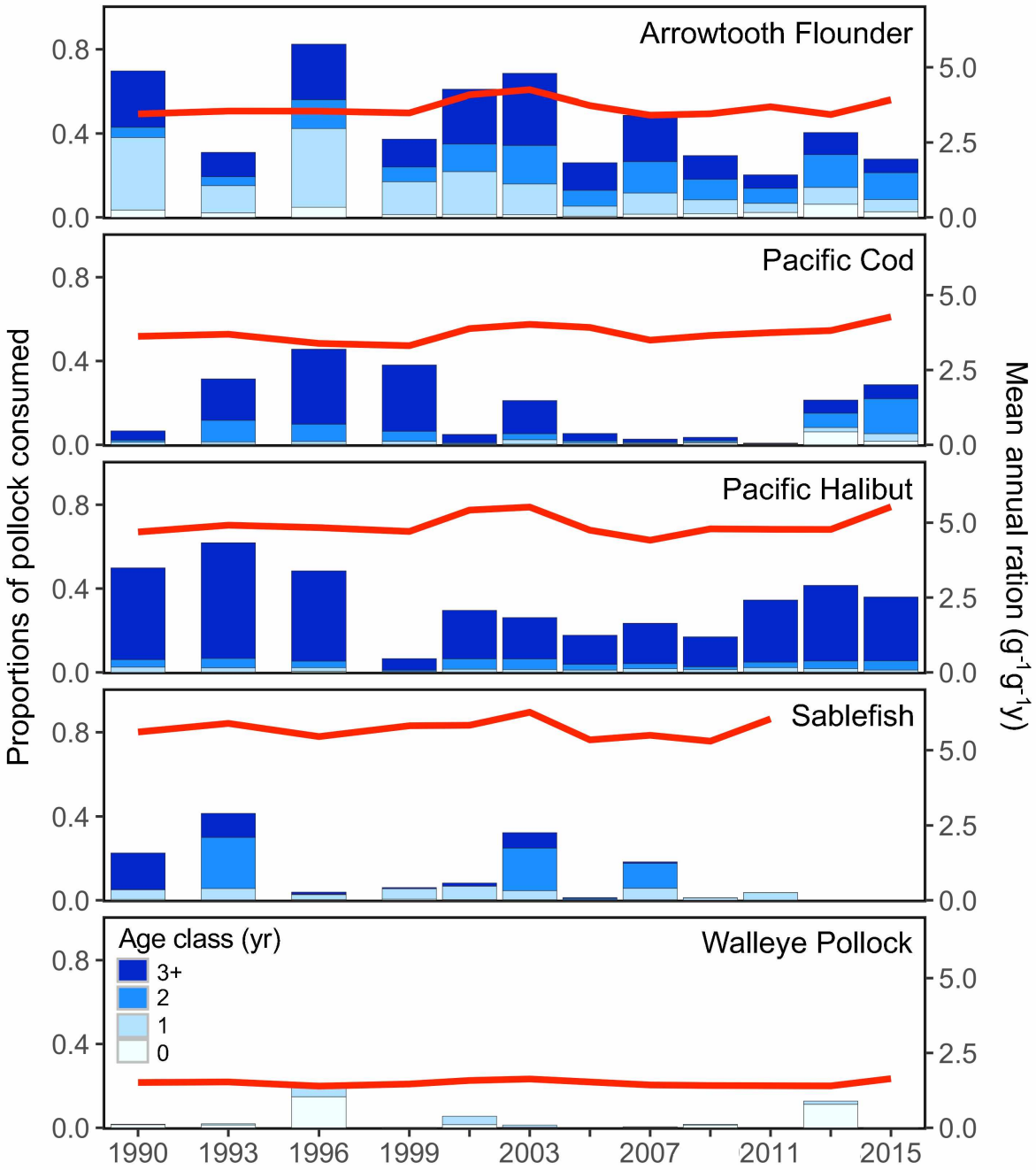

Figure 1.4 Year- and age-specific proportions of pollock consumed ($p_{s,i,j}$, blue bars) and mean annual rations ($\bar{C}_{s,i,j}$; $g^{-1}g^{-1}y$, red lines) by predator and survey year (Gulf of Alaska, 1990 to 2015). Errors bars for mean annual rations have been excluded for clarity.

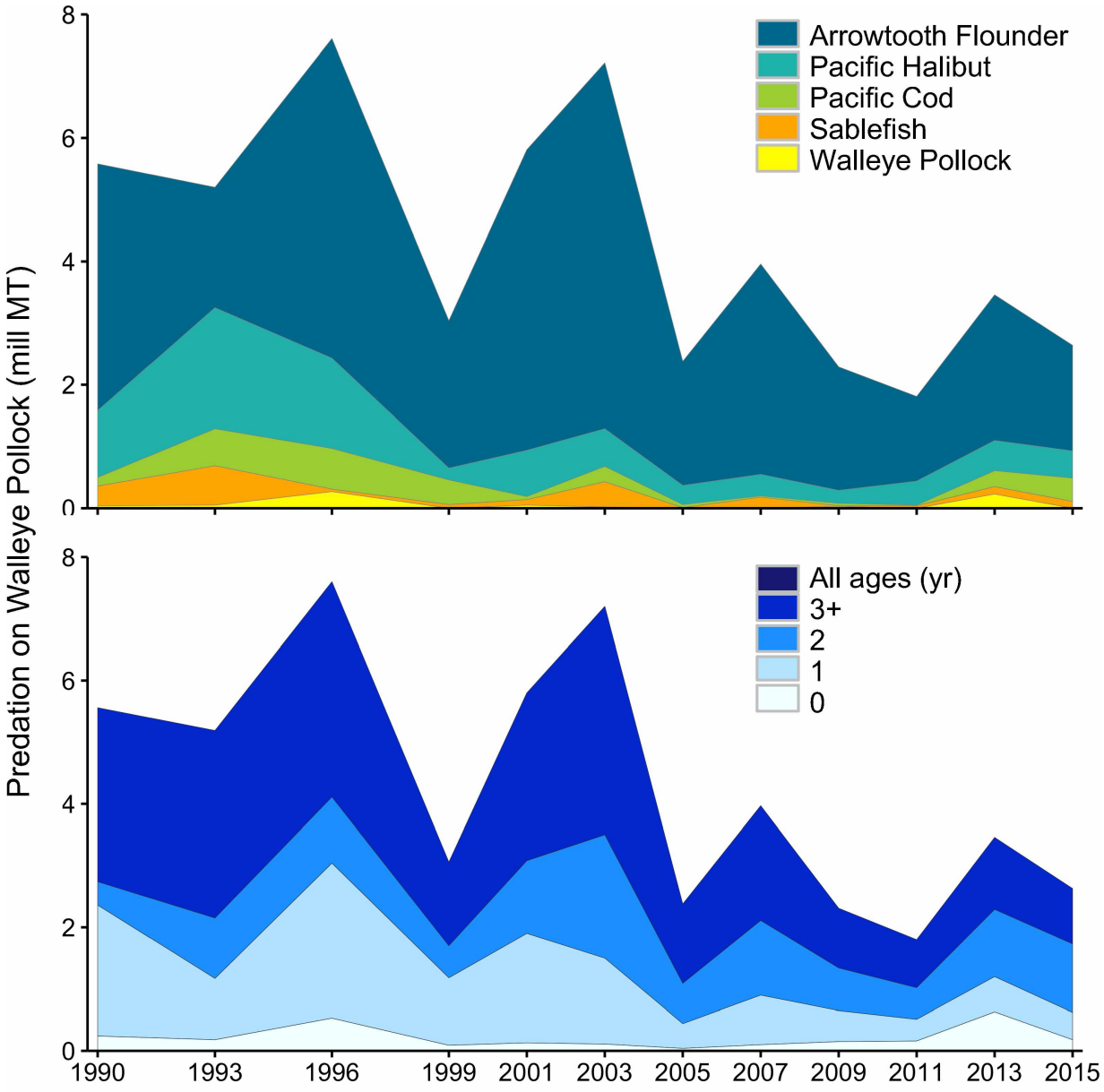

Figure 1.5 Total consumption of Walleye Pollock (millions of metric tons) in the Gulf of Alaska by survey year (1990 to 2015), predator (top; $P_{s,i,j}$), and age class (bottom; $P_{a,i,j}$). Predator-specific indices include all age classes of pollock consumed. Age-specific indices include consumption by all groundfish predators.

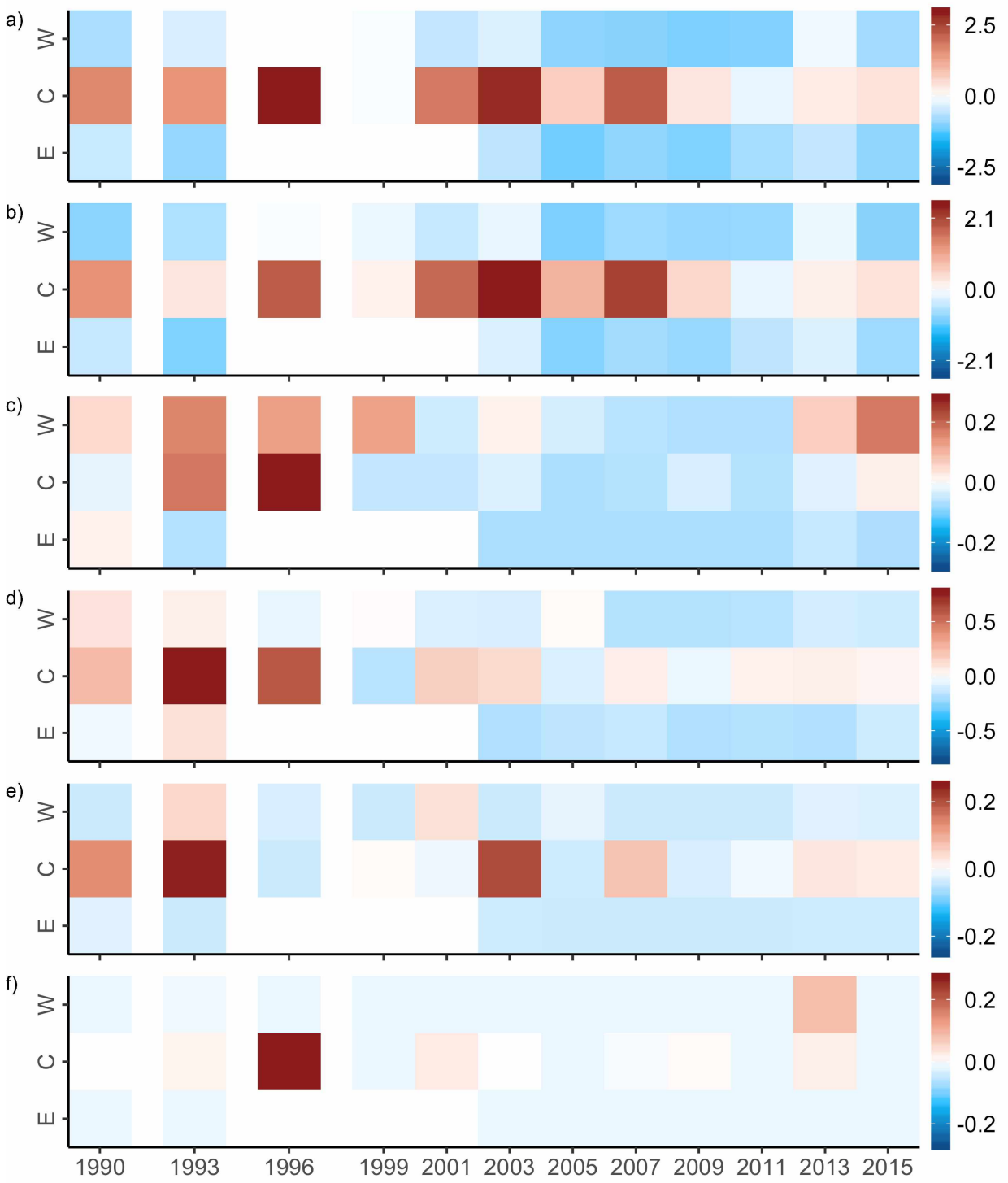

Figure 1.6 Year-specific anomalies in consumption of pollock (relative to the Gulf of Alaska mean) by predator (A: all groundfish predators, B: Arrowtooth Flounder, C: Pacific Cod, D: Pacific Halibut, E: Sablefish, and F: Walleye Pollock) and subregion (W: western, C: central, E: eastern Gulf of Alaska). Positive anomalies (mill MT) are shown in red and negative anomalies (mill MT) are shown in blue. There were no estimates for pollock predation in the eastern Gulf of Alaska between 1996 and 2001.

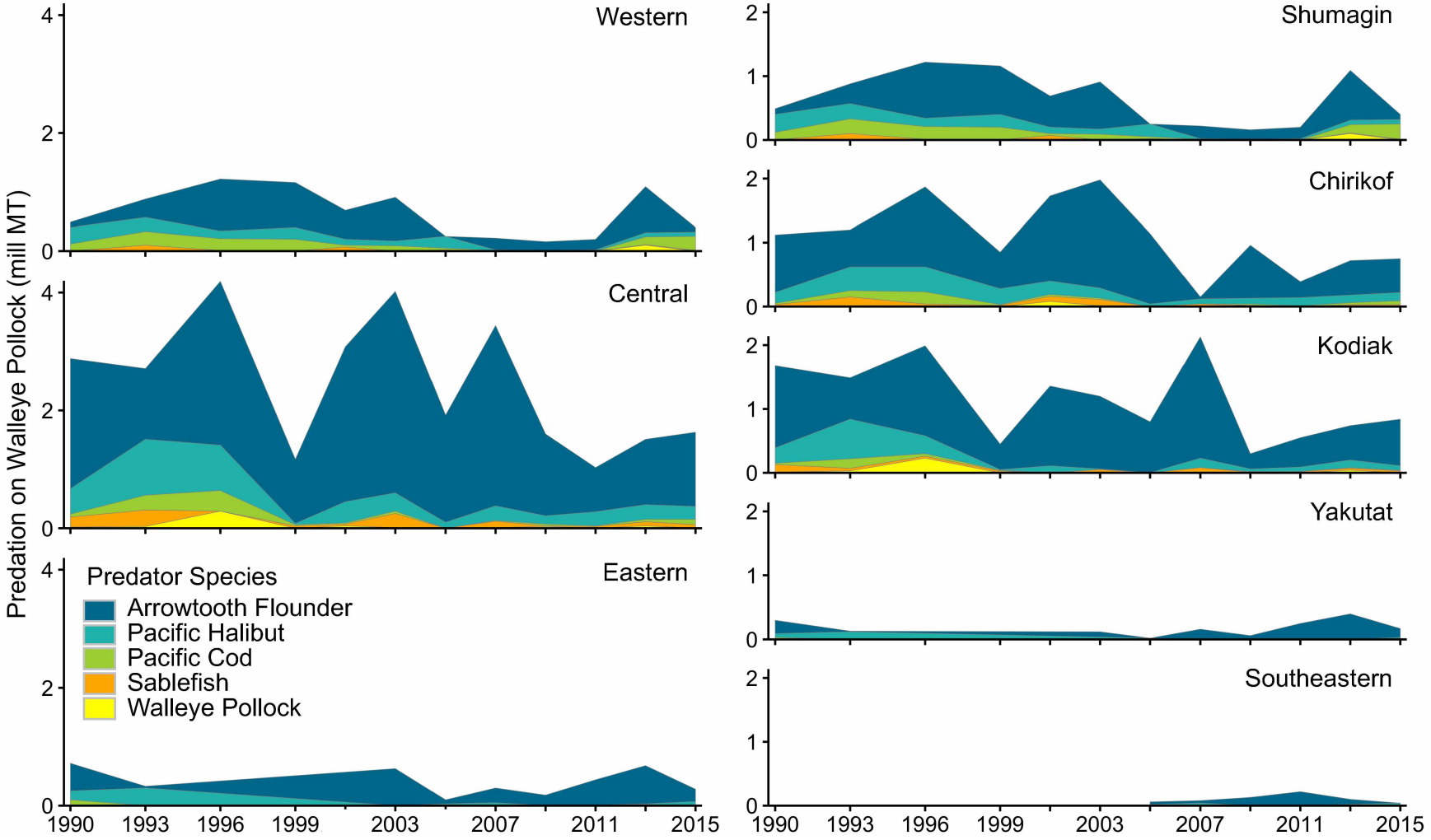

Figure 1.7 Total consumption of Walleye Pollock ($P_{s,i,j}$, mill MT) in the Gulf of Alaska, by survey year (1990 to 2015), predator, subregion (left), and International North Pacific Fisheries Commission (INPFC) statistical area (right). There were no estimates for pollock predation in the eastern Gulf of Alaska between 1996 and 2001, in the Yakutat INPFC statistical from 1996 to 2001, or in the Southeastern statistical area prior to 2005.

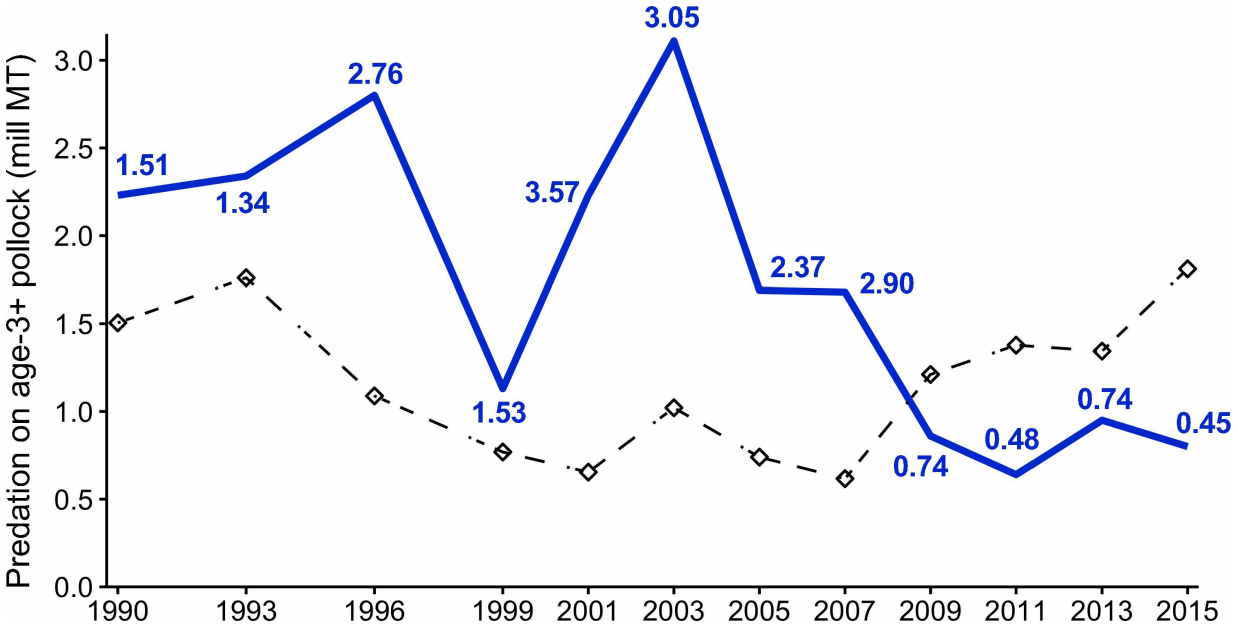

Figure 1.8 Total consumption ($P_{i,j}$, mill MT) of age-3+ pollock (solid blue line) in the area encompassed by the stock assessment for Gulf of Alaska pollock (*i.e.*, Shumagin, Chirikof, Kodiak, and Yakutat statistical areas), 1990 to 2015. Total pollock biomass estimates ($B_{s,i}$, mill MT; diamonds and dashed line) from the most recent stock assessment are also shown (Dorn *et al.* 2017). Numbers indicate the ratio of consumption to biomass in a given year.

1.9 Tables

Table 1.1 Bioenergetics model parameters used to estimate maximum daily consumption (g g^{-1} d^{-1}; Eqn. 2) for each pollock predator (ATF: Arrowtooth Flounder, PC: Pacific Cod, PH: Pacific Halibut, SBL: Sablefish, WEP: Walleye Pollock). Mean estimated number of foraging days ($D_{juvenile}$ or D_{adult}) are also listed, with size ranges used to categorize fish as juveniles or adults shown in parentheses. Superscripts indicate sources of information. Asterisks (*) denote assumed values.

Parameter	ATF [1]	PC [2]	PH [3]	SBL [4]	WEP [1]
C_A	0.125	0.035	0.0625	0.420	0.119
C_B	– 0.1990	– 0.1220	– 0.1076	– 0.3300	– 0.4600
C_Q	2.497	3.079	3.084	2.200	2.600
T_{C_o}	20.512	10.957	12.970	18.000	10.000
T_{C_M}	26.000	25.901	18.000	23.000	15.000
$D_{juvenile}$	346 (< 40 cm)	365 (< 55 cm)	365* (< 82 cm)	365* (< 45 cm)	365 (< 40 cm)
D_{adult}	306 (≥ 40 cm)	329 (≥ 55 cm)	365* (≥ 82 cm)	365* (≥ 45 cm)	365 (≥ 40 cm)

[1] Holsman and Aydin 2015; [2] Holsman *et al.* (in prep); [3] Holsman *et al.* 2019; [4] Harvey 2009

Table 1.2 Total biomass estimates ($B_{s,i}$, MT) from the most recent stock assessments for Arrowtooth Flounder (ATF), Pacific Cod (PC), Pacific Halibut (PH), Sablefish (SBL), and Walleye Pollock (WEP) in the Gulf of Alaska (1990 to 2015). Ages (yr) and lengths (cm) encompassed within total biomass estimates are also shown. Species-specific references are indicated as superscripts. The stock assessment for Pacific Halibut was conducted on a coast-wide basis and included total biomass estimates from 1996 onward. Numbers in parentheses denote biomass scalars based on proportions of halibut ≥ 32 in (82 cm) caught within International Pacific Halibut Commission (IPHC) regulatory areas 4A, 3B, 3A, and 2C during IPHC setline survey. Total halibut biomass was back-calculated for 1990 and 1993 using trends in predicted biomass from the Alaska Fisheries Science Center bottom trawl survey. The Walleye Pollock assessment was partitioned at −140° longitude, with the 'Gulf of Alaska' (^{GOA}) portion to the west and the 'Southeastern' (^{SE}) portion to the east.

Year	ATF [1] 1+ yr; ≥ 19 cm	PC [2] 0+ yr; ≥ 0 cm	PH [3] 8+ yr; ≥ 82 cm	SBL [4] 2+ yr; ≥ 45 cm	WEP [5] 3+ yr; ≥ 37 cm
1990	1,660,800	583,841	1993 * 0.706	251,000	1,479,000 ^{GOA} + 26,101 ^{SE}
1993	1,773,450	516,782	1996 * 1.045	261,000	1,748,000 ^{GOA} + 12,337 ^{SE}
1996	1,770,270	429,292	799,683 (0.782)	200,000	1,013,000 ^{GOA} + 75,596 ^{SE}
1999	1,835,310	320,235	726,201 (0.847)	183,000	737,000 ^{GOA} + 31,836 ^{SE}
2001	1,957,130	286,165	583,773 (0.798)	182,000	625,000 ^{GOA} + 28,979 ^{SE}
2003	2,035,310	292,752	528,888 (0.810)	202,000	1,021,000 ^{GOA} + 26,658 ^{SE}
2005	2,069,910	247,481	432,273 (0.853)	197,000	713,000 ^{GOA} + 36,901 ^{SE}
2007	2,054,040	246,629	406,418 (0.838)	183,000	580,000 ^{GOA} + 41,075 ^{SE}
2009	1,962,540	307,285	351,987 (0.730)	164,000	1,170,000 ^{GOA} + 47,885 ^{SE}
2011	1,826,620	345,269	319,782 (0.742)	181,000	1,330,000 ^{GOA} + 66,969 ^{SE}
2013	1,701,770	316,926	339,740 (0.742)	157,000	1,277,000 ^{GOA} + 39,879 ^{SE}
2015	1,571,460	312,414	301,639 (0.740)	140,000	1,771,000 ^{GOA} + 26,173 ^{SE}

[1] Spies *et al.* 2017; [2] Barbeaux *et al.* 2017; [3] Stewart and Hicks 2017; [4] Hanselman *et al.* 2017; [5] Dorn *et al.* 2017

Table 1.3 Relative predator-specific contributions to overall pollock consumption in the Gulf of Alaska. Values indicate mean proportions (± SD) of overall consumption attributed to each predator species within a given area (1990 to 2015). * The Yakutat and Southeastern statistical areas include survey years between 2005 and 2015 only.

	ATF	PC	PH	SBL	WEP
Basin	0.74 ± 0.14	0.06 ± 0.05	0.16 ± 0.08	0.04 ± 0.03	0.01 ± 0.02
Poll. Assess.	0.76 ± 0.13	0.06 ± 0.05	0.14 ± 0.08	0.03 ± 0.03	0.01 ± 0.02
Western	0.59 ± 0.32	0.16 ± 0.16	0.22 ± 0.23	0.03 ± 0.04	0.01 ± 0.03
Central	0.79 ± 0.14	0.03 ± 0.03	0.14 ± 0.09	0.03 ± 0.03	0.01 ± 0.02
Eastern	0.77 ± 0.29	0.02 ± 0.04	0.21 ± 0.29	0.00 ± 0.00	0.00 ± 0.00
Shumagin	0.59 ± 0.32	0.16 ± 0.16	0.22 ± 0.23	0.03 ± 0.04	0.01 ± 0.03
Chirikof	0.70 ± 0.20	0.03 ± 0.04	0.21 ± 0.14	0.05 ± 0.06	0.01 ± 0.02
Kodiak	0.82 ± 0.15	0.02 ± 0.03	0.12 ± 0.11	0.03 ± 0.02	0.02 ± 0.03
Yakutat *	0.80 ± 0.40	0.00 ± 0.00	0.20 ± 0.40	0.00 ± 0.00	0.00 ± 0.00
Southeastern *	0.66 ± 0.38	0.03 ± 0.08	0.31 ± 0.40	0.00 ± 0.00	0.00 ± 0.00

Table 1.4 Variance ratios VR_j and portfolio effect estimates PE_j (brackets) by spatial scale and time period (Gulf of Alaska, 1990 to 2015). Bolded entries indicate positive portfolio effects. Gray entries denote approximately independent trends (> -0.1 and < 0.1) in pollock consumption among groundfish predators.

Spatial Scale	Time Period		
	1990 to 2015	1990 to 2003	2005 to 2015
Basin	1.42 [- 0.42]	**0.87 [0.13]**	1.20 [- 0.20]
Pollock Assessment Area	1.30 [- 0.30]	**0.87 [0.13]**	0.99 [0.01]
Western	1.30 [- 0.30]	**0.69 [0.31]**	1.36 [- 0.36]
Shumagin	1.30 [- 0.30]	**0.69 [0.31]**	1.36 [- 0.36]
Central	1.34 [- 0.34]	1.17 [- 0.17]	1.03 [- 0.03]
Chirikof	1.30 [- 0.30]	0.97 [0.03]	**0.88 [0.12]**
Kodiak	1.31 [- 0.31]	1.22 [- 0.22]	1.19 [- 0.19]
Eastern	–	–	0.94 [0.06]
Yakutat	–	–	0.95 [0.04]
Southeastern	–	–	**0.64 [0.36]**

Table 1.5 Correlation coefficients representing relationships in pollock consumption among predators (ATF: Arrowtooth Flounder, PC: Pacific Cod, PH: Pacific Halibut, SBL: Sablefish, WEP: Walleye Pollock) in the Gulf of Alaska, 1990 to 2015. Only significant correlations (* $p < 0.1$, ** $p < 0.05$, *** $p < 0.001$) are shown for each area: $_b$ basin, $_p$ area encompassed by the stock assessment for Gulf of Alaska pollock, $_c$ central Gulf of Alaska, $_e$ eastern Gulf of Alaska, $_{chir}$ Chirikof statistical area, and $_{kod}$ Kodiak statistical area.

	ATF	PC	PH	SBL	WEP
ATF	-		-0.78_{se} **	0.51_{kod} *	
PC		-	0.67_b ** 0.63_p ** 0.86_c *** 0.81_{chir} ** 0.93_{kod} ***	0.98_e ***	0.51_b * 0.81_c **
PH			-	0.67_b ** 0.66_p ** 0.60_{chir} **	0.57_c *
SBL				-	0.50_c *
WEP					-

1.10 Supporting Information

1.10.1 Standardized Survey Designs

The AFSC used a stratified random sampling design to conduct standardized surveys along the continental shelf, triennially from 1990 to 1999 and biennially from 2001 to 2015 (von Szalay and Raring 2015; data publicly available at https://www.afsc.noaa.gov/RACE/groundfish/survey_data/data.htm). The Yakutat and Southeastern statistical areas were not surveyed in 2001. Date, location (latitude and longitude), gear depth (m), and bottom temperature (°C) were recorded for each tow. Each species caught was identified and weighed for calculations of catch-per-unit-effort (CPUE; kg per hectare). Fork lengths were measured from a random subsample of 100 to 300 fish per species per haul. Walleye Pollock were also randomly sampled for ageing.

The IPHC started conducting annual setline surveys targeting Pacific Halibut in 1998 (Clark and Hare 2006; data publicly available at https://iphc.int/data/fiss-data-query). Individual setline stations (delineated as 10 nm^2 grid cells) were systematically sampled across the continental shelf, with setline skates deployed in all regulatory areas (*i.e.*, 4A, 3B, 3A, and 2C) throughout the summer. IPHC staff recorded date, latitude, longitude, and gear depth (fm) at each station. Fork lengths (in) were measured and weights (lb) were calculated using known length-weight relationships. CPUE was estimated as the total weight (lb) of halibut caught per effective skate (*i.e.*, 100 standardized circle hooks with 18 ft spacing). For the purposes of this study, we converted depths, lengths, and estimated weights from imperial to metric units (m, cm, g).

The AFSC's Auke Bay Laboratories and RACE Division have jointly administered longline surveys targeting Sablefish and other groundfish species annually since 1979 (Sigler and Zenger 1989; data publicly available at https://www.afsc.noaa.gov/maps/longline/Map.php). Systematic surveys took place in select gullies along the upper continental shelf in summer, beginning in the western Gulf of Alaska and ending in the eastern Gulf of Alaska. AFSC recorded date, latitude, longitude, gear depth (m), and the number of effective skates (*i.e.*, 100 m line with 45 baited circle hooks spaced at 2 m) at each station. Fork length was measured and weight (kg) was calculated from known length-weight regressions.

1.10.2 Food Habits Data Collection

The AFSC subsampled up to five stomachs per species, haul, and size class between 1990 and 2015. The Yakutat statistical area was not subsampled in 1996, 1999, or 2001, the Southeastern statistical area was not subsampled prior to 2005, and Sablefish were not

subsampled in 2013 or 2015. Size classes targeted for stomach content analyses were a) < 31 cm, 31 to 50 cm, 51 to 70 cm, and > 70 cm for Arrowtooth Flounder, Pacific Cod, and Pacific Halibut, b) < 50 cm, 50 to 59 cm, 60 to 69 cm, and ≥ 70 cm for Sablefish, and c) < 30 cm, 30 to 39 cm, 40 to 49 cm, and ≥ 50 cm for Walleye Pollock (Hibpshman *et al.* 2017). Prey from non-empty stomachs were identified to the lowest possible taxonomic group, weighed (0.001 g), and measured by the AFSC's REEM Program (Livingston *et al.* 2017). REEM personnel measured standard lengths (mm) from fish prey, including Walleye Pollock, whenever possible. All data used to calculate proportions of pollock consumed can be found at: https://access.afsc.noaa.gov/REEM/WebDietData/DietDataIntro.php.

1.10.3 Supplemental Figures

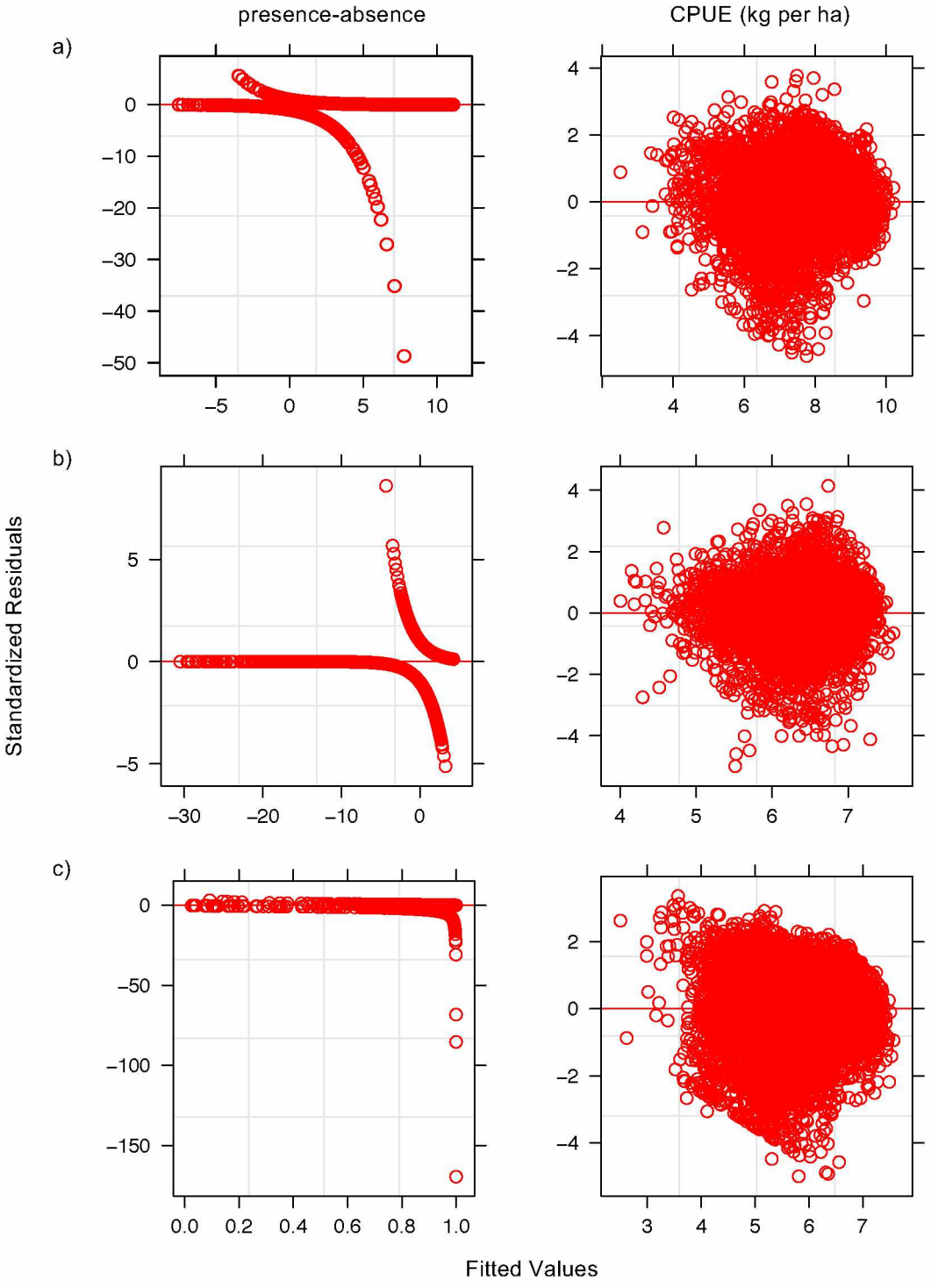

Figure S1.1 Residuals from best-fit generalized additive (mixed) models used to quantify presence-absence (left) and catch-per-unit-effort (CPUE; kg per ha) for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock. Model covariates included survey year (1990 to 2015), latitude and longitude (Gulf of Alaska), depth (m), and bottom temperature (°C).

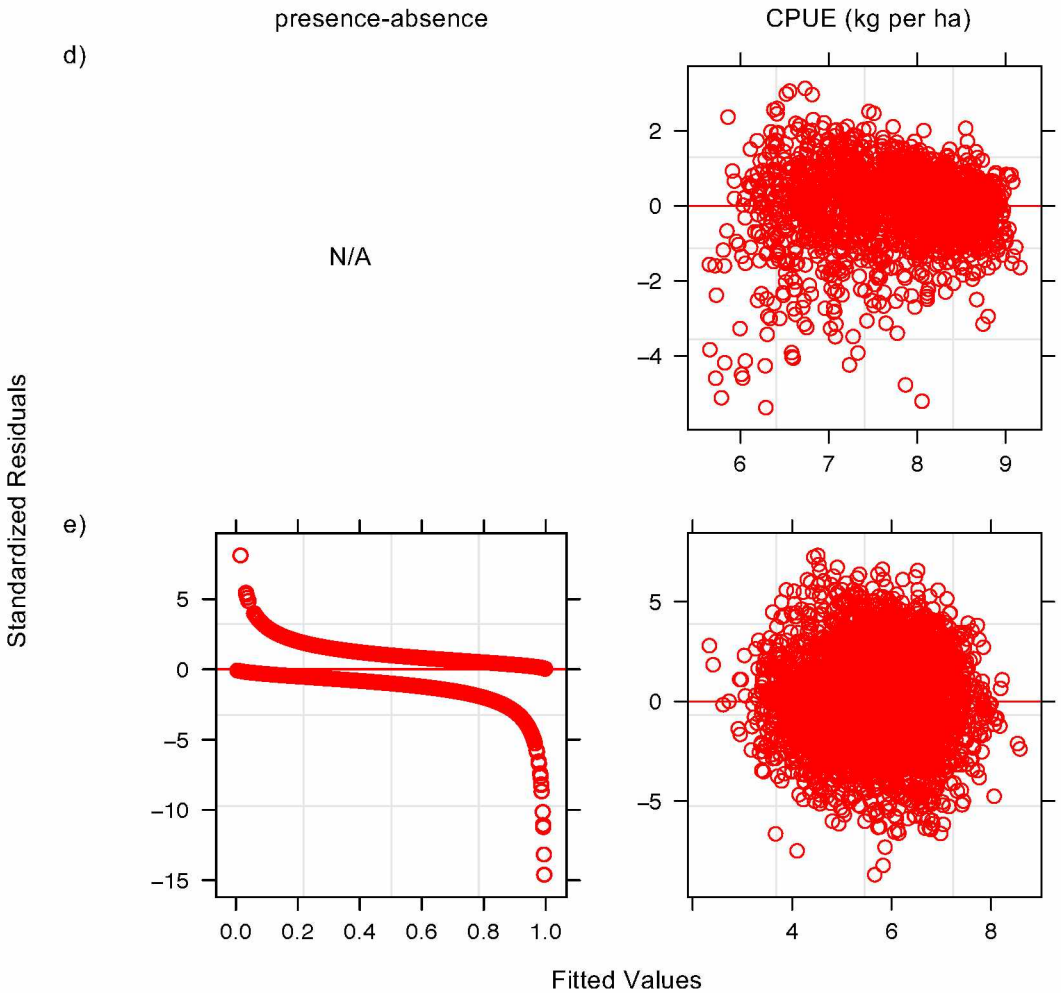

Figure S1.1 (cont) Residuals from best-fit generalized additive (mixed) models used to quantify presence-absence (left) and catch-per-unit-effort (CPUE; kg per ha) for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock. Model covariates included survey year (1990 to 2015), latitude and longitude (Gulf of Alaska), depth (m), and bottom temperature (°C).

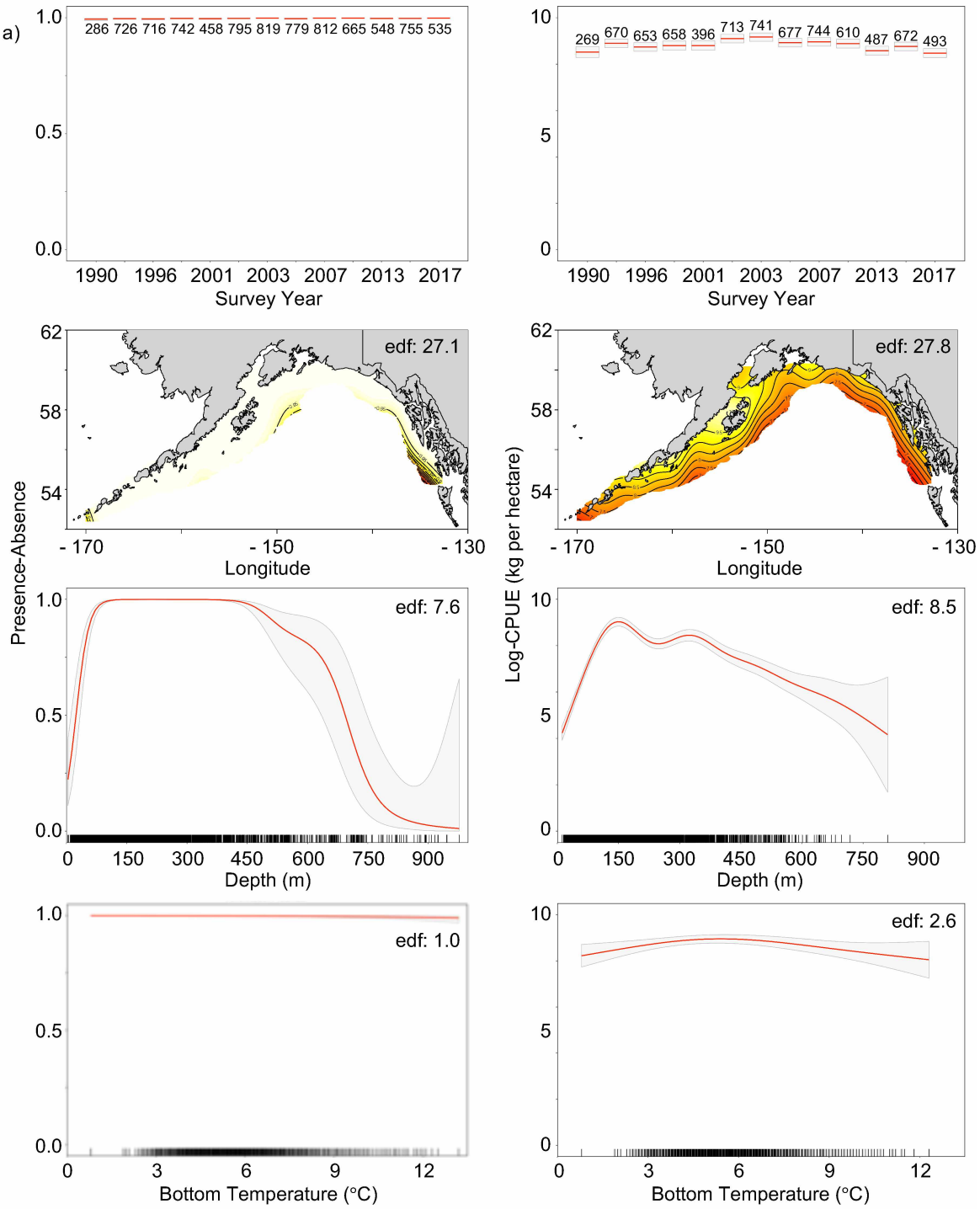

Figure S1.2 Partial effects of model covariates on presence-absence (left) or log-transformed CPUE (right) for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska (1990 to 2015). Red lines show predicted relationships and gray bands denote 95% confidence intervals. Numbers above or below survey years indicate sample sizes. Effective degrees of freedom (EDF) and locations of individual data points (black ticks along x-axes) are shown for smoothed covariates.

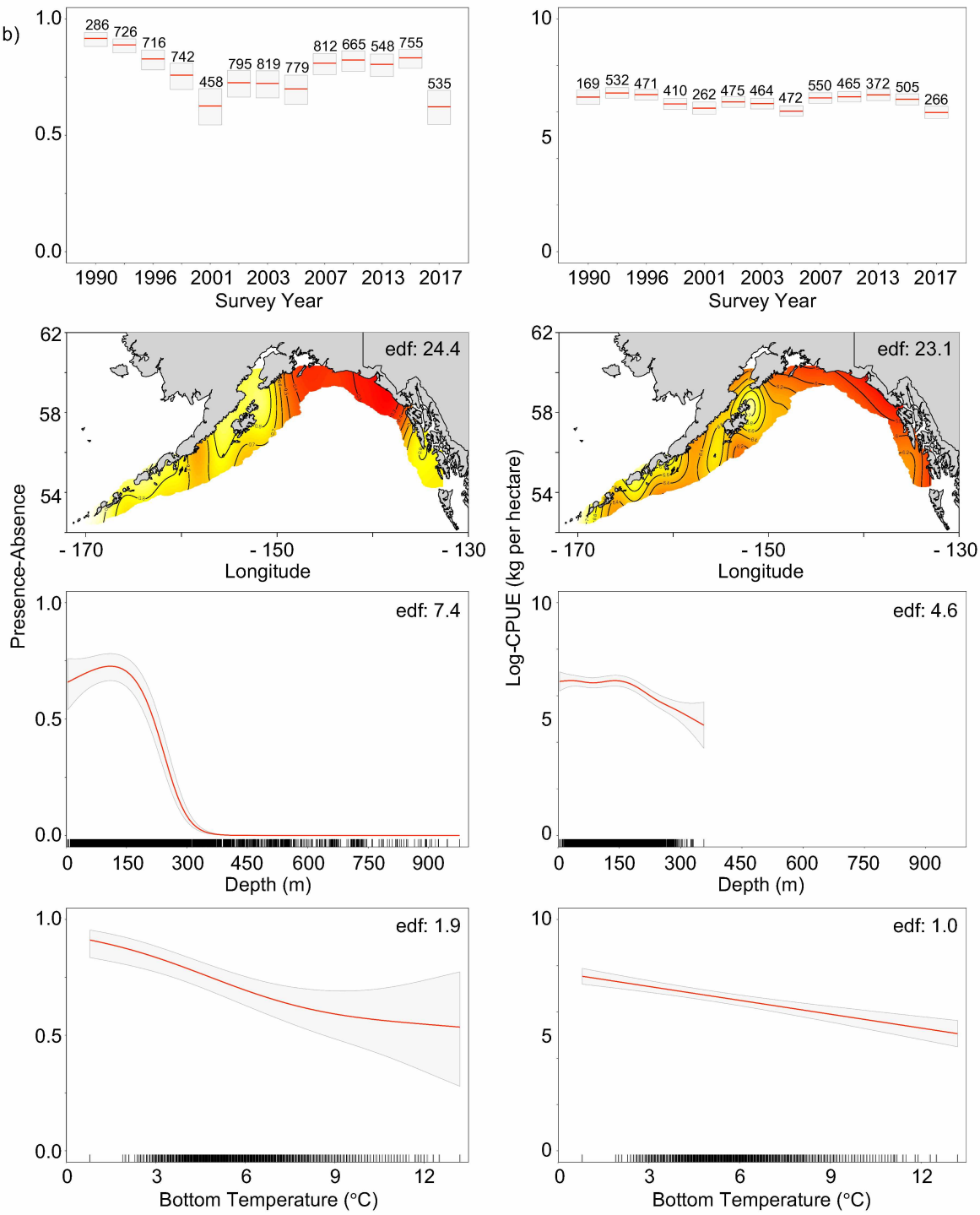

Figure S1.2 (cont) Partial effects of model covariates on presence-absence (left) or log-transformed CPUE (right) for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska (1990 to 2015). Red lines show predicted relationships and gray bands denote 95% confidence intervals. Numbers above or below survey years indicate sample sizes. Effective degrees of freedom (EDF) and locations of individual data points (black ticks along x-axes) are shown for smoothed covariates.

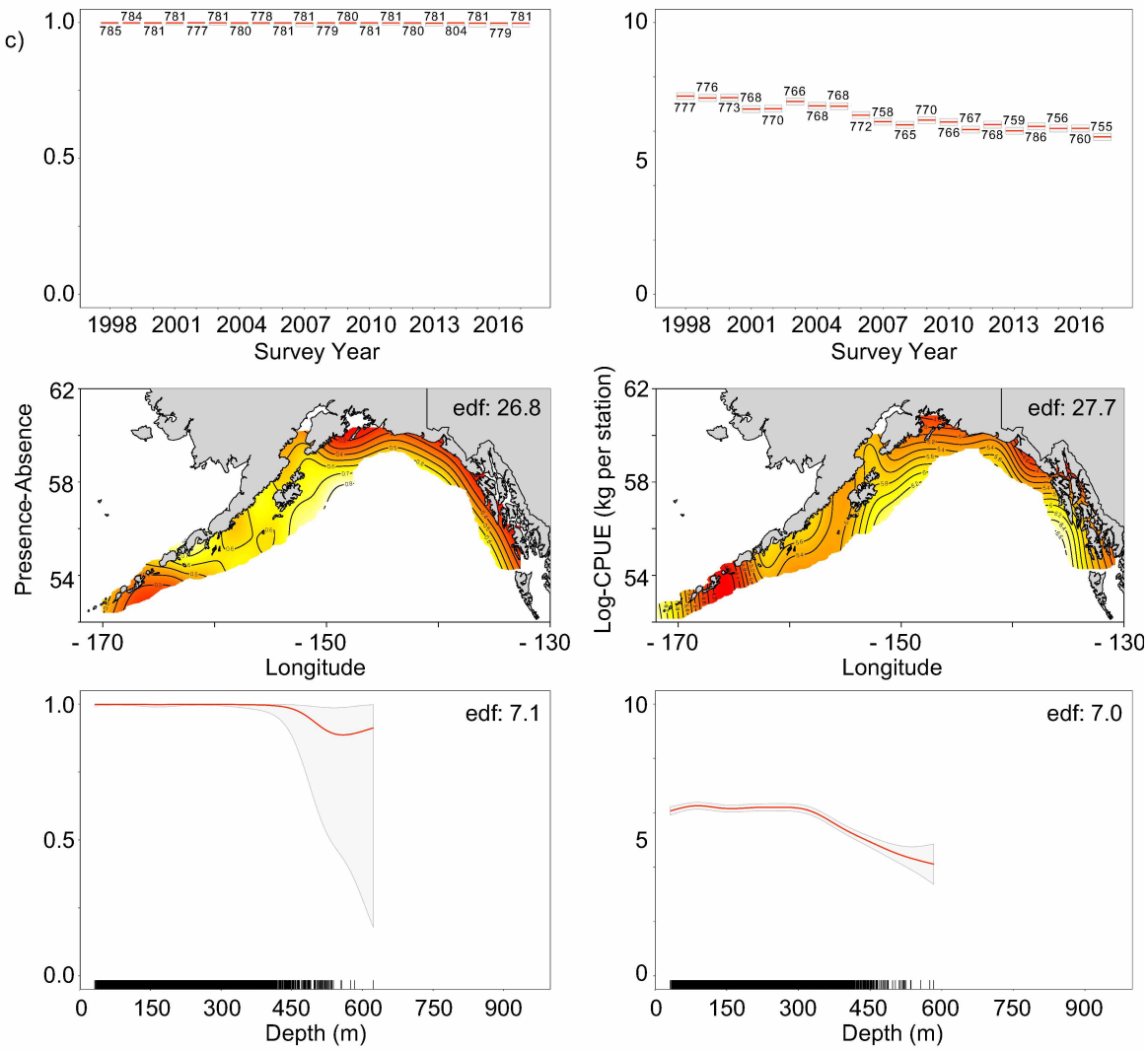

Figure S1.2 (cont) Partial effects of model covariates on presence-absence (left) or log-transformed CPUE (right) for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska (1990 to 2015). Red lines show predicted relationships and gray bands denote 95% confidence intervals. Numbers above or below survey years indicate sample sizes. Effective degrees of freedom (EDF) and locations of individual data points (black ticks along x-axes) are shown for smoothed covariates.

d)

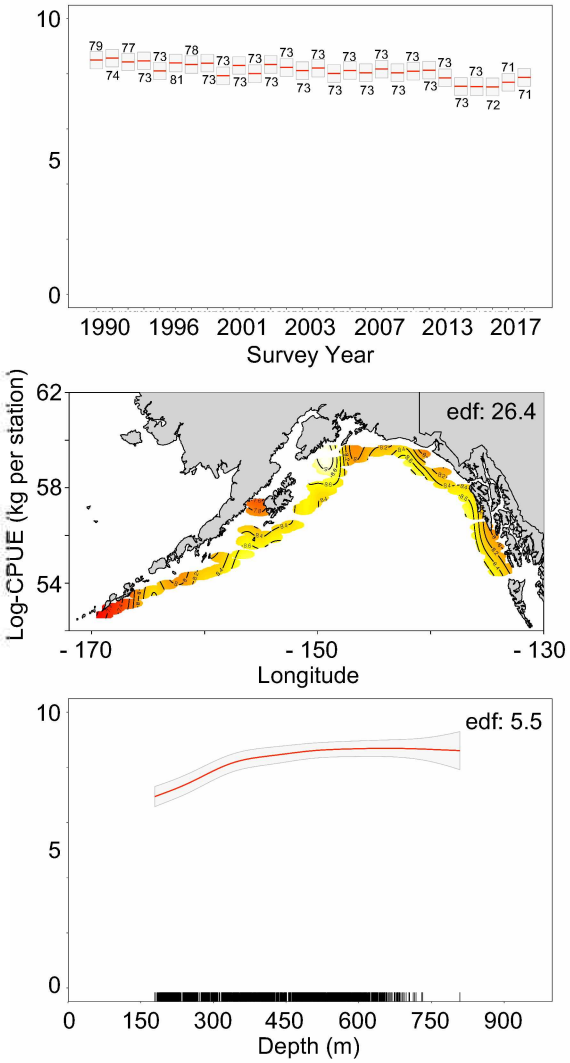

Figure S1.2 (cont) Partial effects of model covariates on presence-absence (left) or log-transformed CPUE (right) for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska (1990 to 2015). Red lines show predicted relationships and gray bands denote 95% confidence intervals. Numbers above or below survey years indicate sample sizes. Effective degrees of freedom (EDF) and locations of individual data points (black ticks along x-axes) are shown for smoothed covariates.

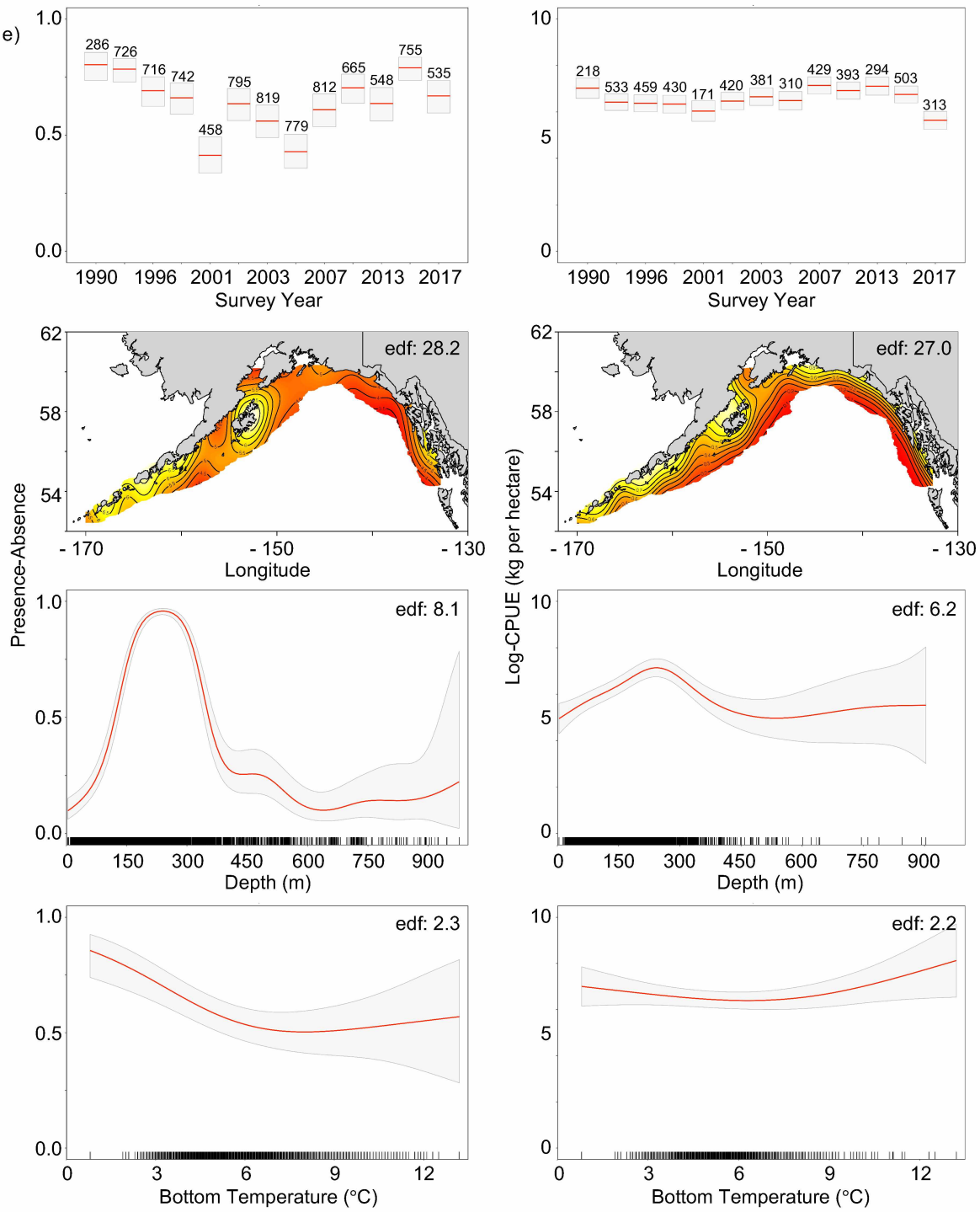

Figure S1.2 (cont) Partial effects of model covariates on presence-absence (left) or log-transformed CPUE (right) for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska (1990 to 2015). Red lines show predicted relationships and gray bands denote 95% confidence intervals. Numbers above or below survey years indicate sample sizes. Effective degrees of freedom (EDF) and locations of individual data points (black ticks along x-axes) are shown for smoothed covariates.

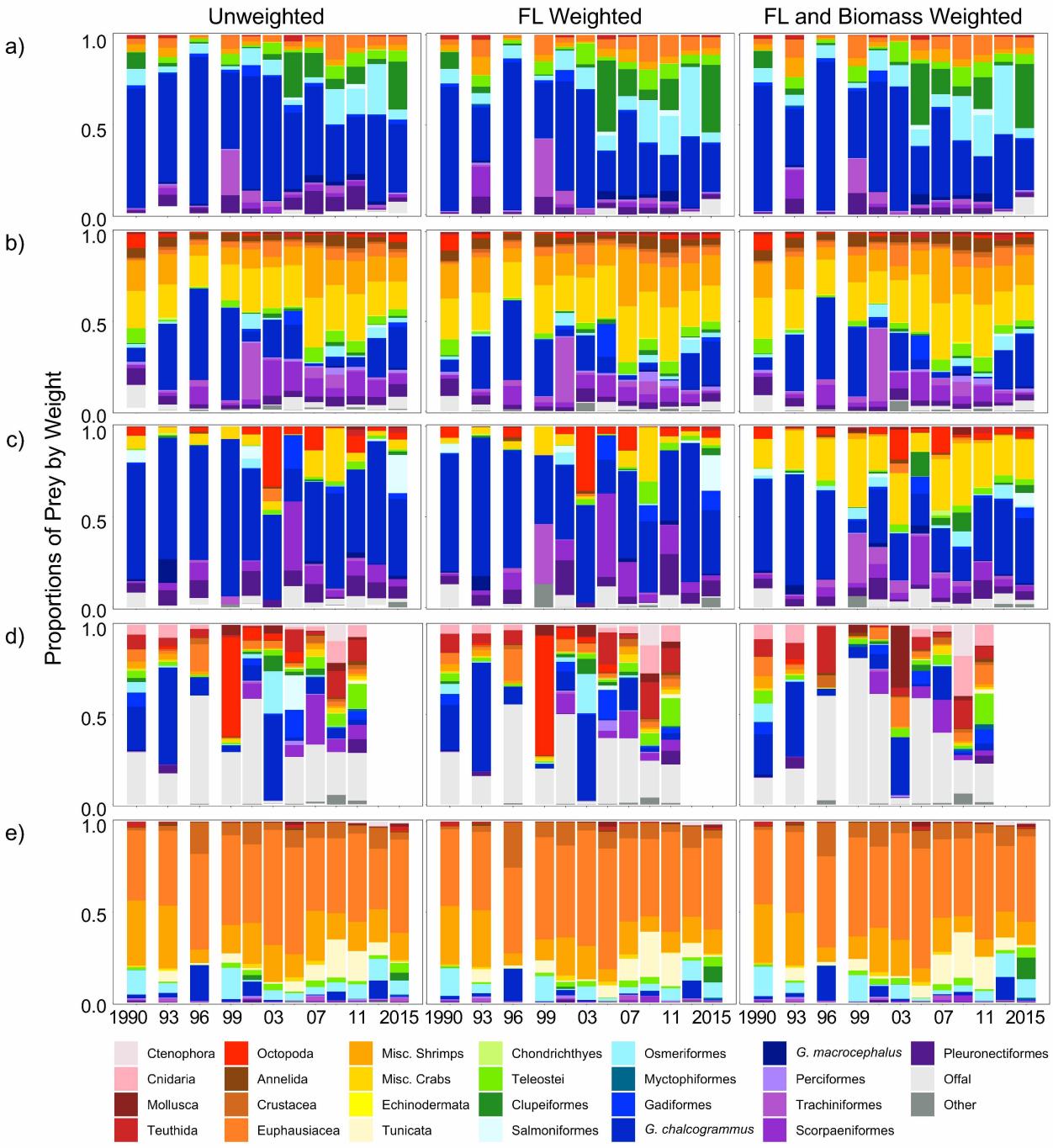

Figure S1.3 Proportions of prey by weight for a) Arrowtooth Flounder ≥ 19 cm, b) Pacific Cod ≥ 0 cm, c) Pacific Halibut ≥ 82 cm, d) Sablefish ≥ 45 cm, and e) Walleye Pollock ≥ 37 cm in the Gulf of Alaska (1990 to 2015). Proportional diet compositions are shown as unweighted (left panel), fork length-weighted (FL; middle panel), and fork length- and biomass-weighted (right panel).

1.10.4 Supplemental Tables

Table S1.1 Parameters α and β used to estimate weight from length for Arrowtooth Flounder (ATF), Pacific Cod (PC), Sablefish (SBL; f: female, m: male), and Walleye Pollock (WEP). The bias-correction factor for Walleye Pollock and references for species-specific relationships are also shown. Individual weights for Pacific Halibut were provided by the International Pacific Halibut Commission's setline survey.

Species	α	β	cf	Reference
ATF	4.312×10^{-3}	3.1860	-	Spies *et al.* 2017
PC	5.631×10^{-6}	3.1306	-	Barbeaux *et al.* 2017
SBL_f	1.010×10^{-5}	3.0150	-	Hanselman *et al.* 2007
SBL_m	1.240×10^{-5}	2.9600	-	Hanselman *et al.* 2007
WEP	5.616×10^{-6}	3.0447	1.007	Dorn *et al.* 2017; Brodziak 2012

Table S1.2 Results for the top three generalized additive models used to quantify presence-absence and log-transformed CPUE of positive catches, by species. X indicates variables (survey year, longitude and latitude, depth [m], bottom temperature [°C]) included in each alternative model. The deviance explained (Dev. %), equivalent degrees of freedom (edf), log-likelihood (LL), Δ AIC, Akaike weight (W_i), and unbiased risk estimator (UBRE) are noted. Selected models are shown in bold.

	Variables Included									
Model	Year	Lon, Lat	Depth	Temp	Dev. (%)	edf	LL	ΔAIC	W_i	GCV / UBRE
Arrowtooth Flounder presence-absence	**X**	**X**	**X**	**X**	**44.9**	**49**	**- 1534**	**0.0**	**0.998**	**- 0.633**
	X	X	X		44.6	48	- 1541	12.7	0.002	- 0.632
		X	X	X	43.8	37	- 1566	40.3	0.000	- 0.629
CPUE, where present	**X**	**X**	**X**	**X**	**36.0**	**52**	**- 13869**	**0.0**	**1.000**	**2.095**
	X	X	X		35.8	50	- 13881	18.6	0.000	2.100
		X	X	X	34.8	40	- 13937	112.9	0.000	2.125
Pacific Cod presence-absence	**X**	**X**	**X**	**X**	**29.8**	**45**	**- 4007**	**0.0**	**1.000**	**- 0.062**
	X	X	X		29.5	42	- 4020	22.2	0.000	- 0.059
		X	X	X	27.2	33	- 4152	267.0	0.000	- 0.031
CPUE, where present	**X**	**X**	**X**	**X**	**11.0**	**47**	**- 10121**	**0.0**	**1.000**	**2.506**
	X	X	X		10.4	47	- 10137	32.3	0.000	2.521
	X	X		X	9.4	41	- 10167	81.1	0.000	2.544
Pacific Halibut presence-absence	**X**	**X**	**X**	**-**	**36.8**	**54**	**- 924**	**0.0**	**1.000**	**- 0.875**
		X	X	-	35.0	34	- 952	16.5	0.000	- 0.874
	X	X		-	31.1	48	- 1008	155.6	0.000	- 0.865
CPUE, where present	**X**	**X**	**X**	**-**	**32.0**	**56**	**- 21128**	**0.0**	**1.000**	**0.925**
	X	X		-	30.7	48	- 21275	278.5	0.000	0.942
	X		X	-	17.5	25	- 22615	2912.2	0.000	1.119

Table S1.2 (cont) Results for the top three generalized additive models used to quantify presence-absence and log-transformed CPUE of positive catches, by species. X indicates variables (survey year, longitude and latitude, depth [m], bottom temperature [°C]) included in each alternative model. The deviance explained (Dev. %), equivalent degrees of freedom (df), log-likelihood (LL), Δ AIC, Akaike weight (W_i), and unbiased risk estimator (UBRE) are noted. Selected models are shown in bold.

	Variables Included in Alt. Model									
Model	Year	Lon, Lat	Depth	Temp	Dev. (%)	edf	LL	ΔAIC	W_i	GCV / UBRE
Sablefish										
presence-absence	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
CPUE, where present	**X**	**X**	**X**	**-**	**63.2**	**62**	**- 1762**	**0.00**	**1.000**	**0.343**
		X	X	-	54.1	34	- 1991	401.9	0.000	0.417
	X	X		-	53.6	57	- 2002	469.8	0.000	0.431
Walleye Pollock										
presence-absence	**X**	**X**	**X**	**X**	**28.3**	**52**	**- 4244**	**0.0**	**1.000**	**- 0.005**
	X	X	X		28.1	49	- 4257	21.7	0.000	- 0.003
		X	X	X	25.6	39	- 4406	298.8	0.000	0.029
CPUE, where present	**X**	**X**	**X**	**X**	**15.3**	**50**	**- 10616**	**0.0**	**0.971**	**4.744**
	X	X	X		15.1	47	- 10622	7.0	0.029	4.751
		X	X	X	12.7	38	- 10690	124.7	0.000	4.867

Table S1.3 Parameter estimates from best-fit generalized additive models quantifying presence-absence and CPUE for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska. Year was treated as a factor. Thus, 1990 is denoted as the model intercept except in the case of Pacific Halibut, where the intercept represents 1998. Subsequent estimates for year are shown as differences from the model intercept. Although there were additional survey years for Pacific Halibut and Sablefish models, only years with bottom trawl survey data are shown. Non-significant terms ($\alpha = 0.1$) are in gray.

a) Arrowtooth Flounder

Model	Estimate	Std. Error	z- or t-value	edf	Chi Sq. or F	p-value	Adj. R^2
Presence-Absence							0.408
(intercept)	3.35	0.32	10.58			< 0.001	
1993	0.44	0.35	1.24			0.214	
1996	0.15	0.35	0.45			0.656	
1999	0.66	0.36	1.85			0.065	
2001	0.46	0.36	1.26			0.208	
2003	0.84	0.35	2.42			0.015	
2005	1.32	0.35	3.74			< 0.001	
2007	0.43	0.35	1.22			0.221	
2009	1.18	0.36	3.26			0.001	
2011	1.28	0.36	3.52			< 0.001	
2013	0.64	0.36	1.77			0.077	
2015	0.91	0.35	2.58			0.010	
2017	1.22	0.38	3.25			0.001	
Lon, Lat				28.23	371.75	< 0.001	
Depth				7.17	759.06	< 0.001	
Bottom Temp				1.08	15.34	< 0.001	
CPUE, kg per ha							0.355
(intercept)	7.10	0.09	78.50			< 0.001	
1993	0.38	0.11	3.63			< 0.001	
1996	0.22	0.11	2.07			0.039	
1999	0.31	0.11	2.86			0.004	
2001	0.27	0.12	2.30			0.022	
2003	0.59	0.11	5.49			< 0.001	
2005	0.65	0.11	6.15			< 0.001	
2007	0.41	0.11	3.77			< 0.001	
2009	0.45	0.11	4.20			< 0.001	
2011	0.38	0.11	3.46			< 0.001	
2013	0.06	0.11	0.49			0.622	
2015	0.25	0.11	2.32			0.020	
2017	- 0.05	0.11	- 0.42			0.677	
Lon, Lat				28.37	55.82	< 0.001	
Depth				8.02	239.55	< 0.001	
Bottom Temp				2.53	8.20	< 0.001	

Table S1.3 (cont) Parameter estimates from best-fit generalized additive models quantifying presence-absence and CPUE for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska. Year was treated as a factor. Thus, 1990 is denoted as the model intercept except in the case of Pacific Halibut, where the intercept represents 1998. Subsequent estimates for year are shown as differences from the model intercept. Although there were additional survey years for Pacific Halibut and Sablefish models, only years with bottom trawl survey data are shown. Non-significant terms (α = 0.1) are in gray.

b) Pacific Cod

Model	Estimate	Std. Error	z- or t-value	edf	Chi Sq. or F	p-value	Adj. R^2
Presence-Absence							0.348
(intercept)	0.96	0.50	1.90			0.058	
1993	- 0.34	0.19	- 1.80			0.072	
1996	- 0.84	0.19	- 4.45			< 0.001	
1999	- 1.27	0.19	- 6.69			< 0.001	
2001	- 1.90	0.20	- 9.64			< 0.001	
2003	- 1.44	0.19	- 7.78			< 0.001	
2005	- 1.46	0.18	- 7.93			< 0.001	
2007	- 1.57	0.19	- 8.22			< 0.001	
2009	- 0.97	0.19	- 5.05			< 0.001	
2011	- 0.87	0.19	- 4.50			< 0.001	
2013	- 0.99	0.20	- 4.98			< 0.001	
2015	- 0.82	0.19	- 4.31			< 0.001	
2017	- 1.91	0.19	- 9.87			< 0.001	
Lon, Lat				25.67	821.80	< 0.001	
Depth				4.58	552.30	< 0.001	
Bottom Temp				2.07	25.50	< 0.001	
CPUE, kg per ha							0.102
(intercept)	6.44	0.13	51.12			< 0.001	
1993	0.18	0.14	1.27			0.206	
1996	0.10	0.15	0.67			0.504	
1999	- 0.28	0.15	- 1.84			0.066	
2001	- 0.49	0.16	- 3.01			0.003	
2003	- 0.21	0.15	- 1.39			0.163	
2005	- 0.28	0.15	- 1.88			0.060	
2007	- 0.59	0.15	- 3.93			< 0.001	
2009	- 0.03	0.15	- 0.20			0.840	
2011	0.02	0.15	0.12			0.906	
2013	0.10	0.15	0.65			0.514	
2015	- 0.09	0.15	- 0.63			0.531	
2017	- 0.67	0.16	- 4.17			< 0.001	
Lon, Lat				25.20	6.99	< 0.001	
Depth				7.08	11.81	< 0.001	
Bottom Temp				1.37	25.51	< 0.001	

Table S1.3 (cont) Parameter estimates from best-fit generalized additive models quantifying presence-absence and CPUE for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska. Year was treated as a factor. Thus, 1990 is denoted as the model intercept except in the case of Pacific Halibut, where the intercept represents 1998. Subsequent estimates for year are shown as differences from the model intercept. Although there were additional survey years for Pacific Halibut and Sablefish models, only years with bottom trawl survey data are shown. Non-significant terms ($\alpha = 0.1$) are in gray.

c) Pacific Halibut

Model	Estimate	Std. Error	z- or t-value	edf	Chi Sq. or F	p-value	Adj. R^2
Presence-Absence							0.218
(intercept)	6.74	0.45	15.00			< 0.001	
1993	-	-	-			-	
1996	-	-	-			-	
1999	- 0.04	0.56	- 0.08			0.939	
2001	- 0.76	0.50	- 1.52			0.130	
2003	- 0.87	0.49	- 1.78			0.075	
2005	- 0.58	0.51	- 1.13			0.257	
2007	- 1.43	0.46	- 3.07			0.002	
2009	- 0.33	0.53	- 0.63			0.530	
2011	- 0.95	0.49	- 1.95			0.051	
2013	- 1.38	0.46	- 2.97			0.003	
2015	- 1.50	0.46	- 3.26			0.001	
2017	- 1.58	0.46	- 3.47			< 0.001	
Lon, Lat				26.75	439.2	< 0.001	
Depth				7.06	152.1	< 0.001	
Bottom Temp				-	-	-	
CPUE, kg per ha							0.318
(intercept)	6.53	0.03	189.67			< 0.001	
1993	-	-	-			-	
1996	-	-	-			-	
1999	- 0.07	0.05	- 1.35			0.178	
2001	- 0.48	0.05	- 9.78			< 0.001	
2003	- 0.20	0.05	- 4.09			< 0.001	
2005	- 0.37	0.05	- 7.58			< 0.001	
2007	- 0.93	0.05	- 18.98			< 0.001	
2009	- 0.90	0.05	- 18.49			< 0.001	
2011	- 1.25	0.05	- 25.49			< 0.001	
2013	- 1.30	0.05	- 26.54			< 0.001	
2015	- 1.22	0.05	- 24.85			< 0.001	
2017	- 1.53	0.05	- 31.20			< 0.001	
Lon, Lat				27.96	111.91	< 0.001	
Depth				7.80	34.42	< 0.001	
Bottom Temp				-	-	-	

Table S1.3 (cont) Parameter estimates from best-fit generalized additive models quantifying presence-absence and CPUE for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska. Year was treated as a factor. Thus, 1990 is denoted as the model intercept except in the case of Pacific Halibut, where the intercept represents 1998. Subsequent estimates for year are shown as differences from the model intercept. Although there were additional survey years for Pacific Halibut and Sablefish models, only years with bottom trawl survey data are shown. Non-significant terms ($\alpha = 0.1$) are in gray.

d) Sablefish

Model	Estimate	Std. Error	z- or t-value	edf	Chi Sq. or F	p-value	Adj. R^2
Presence-Absence							-
(intercept)	-	-	-			-	
1993	-	-	-			-	
1996	-	-	-			-	
1999	-	-	-			-	
2001	-	-	-			-	
2003	-	-	-			-	
2005	-	-	-			-	
2007	-	-	-			-	
2009	-	-	-			-	
2011	-	-	-			-	
2013	-	-	-			-	
2015	-	-	-			-	
2017	-	-	-			-	
Lon, Lat				-	-	-	
Depth				-	-	-	
Bottom Temp				-	-	-	
CPUE, kg per ha							0.621
(intercept)	8.16	0.07	125.15			< 0.001	
1993	- 0.02	0.09	- 0.26			0.798	
1996	- 0.16	0.09	- 1.69			0.091	
1999	- 0.19	0.09	- 2.02			0.044	
2001	- 0.16	0.09	- 1.66			0.098	
2003	- 0.38	0.09	- 4.02			< 0.001	
2005	- 0.48	0.09	- 5.13			< 0.001	
2007	- 0.46	0.09	- 4.85			< 0.001	
2009	- 0.45	0.09	- 4.83			< 0.001	
2011	- 0.36	0.09	- 3.84			< 0.001	
2013	- 0.95	0.09	- 10.11			< 0.001	
2015	- 0.97	0.09	- 10.26			< 0.001	
2017	- 0.63	0.09	- 6.62			< 0.001	
Lon, Lat				27.37	25.95	< 0.001	
Depth				6.11	78.02	< 0.001	
Bottom Temp				-	-	-	

Table S1.3 (cont) Parameter estimates from best-fit generalized additive models quantifying presence-absence and CPUE for a) Arrowtooth Flounder, b) Pacific Cod, c) Pacific Halibut, d) Sablefish, and e) Walleye Pollock in the Gulf of Alaska. Year was treated as a factor. Thus, 1990 is denoted as the model intercept except in the case of Pacific Halibut, where the intercept represents 1998. Subsequent estimates for year are shown as differences from the model intercept. Although there were additional survey years for Pacific Halibut and Sablefish models, only years with bottom trawl survey data are shown. Non-significant terms ($\alpha = 0.1$) are in gray.

e) Walleye Pollock

Model	Estimate	Std. Error	z- or t-value	edf	Chi Sq. or F	p-value	Adj. R^2
Presence-Absence							0.342
(intercept)	1.24	0.16	7.52			< 0.001	
1993	- 0.12	0.19	- 0.64			0.524	
1996	- 0.61	0.19	- 3.24			0.001	
1999	- 0.74	0.19	- 3.92			< 0.001	
2001	- 1.77	0.21	- 8.62			< 0.001	
2003	- 0.87	0.19	- 4.64			< 0.001	
2005	- 1.17	0.18	- 6.34			< 0.001	
2007	- 1.70	0.19	- 8.89			< 0.001	
2009	- 0.97	0.19	- 5.13			< 0.001	
2011	- 0.55	0.19	- 2.87			0.004	
2013	- 0.85	0.20	- 4.38			< 0.001	
2015	- 0.09	0.19	- 0.47			0.642	
2017	- 0.71	0.20	- 3.62			< 0.001	
Lon, Lat				28.17	636.94	< 0.001	
Depth				8.13	1372.48	< 0.001	
Bottom Temp				2.35	24.94	< 0.001	
CPUE, kg per ha							0.144
(intercept)	6.05	0.15	39.71			< 0.001	
1993	- 0.62	0.18	- 3.48			< 0.001	
1996	- 0.66	0.18	- 3.58			< 0.001	
1999	- 0.67	0.19	- 3.53			< 0.001	
2001	- 0.99	0.23	- 4.33			< 0.001	
2003	- 0.58	0.19	- 3.08			0.002	
2005	- 0.31	0.19	- 1.63			0.103	
2007	- 0.54	0.20	- 2.68			0.007	
2009	0.14	0.19	0.74			0.458	
2011	- 0.09	0.19	- 0.47			0.639	
2013	0.11	0.20	0.57			0.570	
2015	- 0.28	0.18	- 1.52			0.128	
2017	- 1.36	0.20	- 6.91			< 0.001	
Lon, Lat				28.26	20.15	< 0.001	
Depth				5.92	24.01	< 0.001	
Bottom Temp				2.41	2.47	0.037	

Table S1.4. Akaike information criterion (expressed as ΔAIC) for generalized additive mixed models (GAMM) with and without a Gaussian spatial autocorrelation term for Arrowtooth Flounder (ATF), Pacific Cod (PC), Pacific Halibut (PH), Sablefish (SBL), and Walleye Pollock (WEP). Equivalent degrees of freedom (rounded to the nearest whole number) are shown in parentheses. Selected models shown in bold. GAMMs would not converge when modeling presence-absence for Pacific Halibut. Sablefish were observed at nearly all stations, eliminating the need to model presence-absence for this species.

	Presence-Absence		log-CPUE	
Model	GAMM w/	GAMM w/o	GAMM w/	GAMM w/o
ATF	**0 (49)**	317 (48)	**0 (52)**	25 (52)
PC	**0 (47)**	144 (43)	**0 (42)**	7 (42)
PH	-	-	**0 (55)**	980 (54)
SBL	N/A	N/A	2 (60)	**0 (60)**
WEP	7 (51)	**0 (51)**	**0 (48)**	37 (48)

Table S1.5 Relative foraging rates (RFR; proportion of C_{max}) for Arrowtooth Flounder, Pacific Cod, Pacific Halibut, Sablefish, and Walleye Pollock in the Gulf of Alaska. References for each size-specific estimate are also shown.

Predator	RFR	Reference
Arrowtooth Flounder	< 40 cm: 0.79 ≥ 40 cm: 1.07	Holsman and Aydin 2015
Pacific Cod	< 55 cm: 0.41 ≥ 55 cm: 0.47	Holsman and Aydin 2015
Pacific Halibut	< 40 cm: 0.26 40 – 120 cm: 0.40	Holsman *et al.* 2019
Sablefish	40 – 50 cm: 0.27 ≥ 50 cm: 0.26	Harvey 2009
Walleye Pollock	< 40 cm: 0.49 ≥ 40 cm: 0.56	Holsman and Aydin 2015

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Chapter 2 Assessing the potential for competition between Pacific Halibut (*Hippoglossus stenolepis*) and Arrowtooth Flounder (*Atheresthes stomias*) in the Gulf of Alaska [2]

2.1 Abstract

Pacific Halibut (*Hippoglossus stenolepis*) support culturally and economically important fisheries in the Gulf of Alaska, though recent decreases in mean size-at-age have substantially reduced fishery yields, generating concerns among stakeholders and resource managers. Among the prevailing hypotheses for reduced size-at-age is intensified competition with Arrowtooth Flounder (*Atheresthes stomias*), a groundfish predator that exhibited nearly five-fold increases in biomass between the 1960s and mid-2010s. To assess the potential for competition between Pacific Halibut and Arrowtooth Flounder, we evaluated their degree of spatiotemporal and dietary overlap in the Gulf of Alaska using bottom trawl survey and food habits data provided by the Alaska Fisheries Science Center, NOAA (1990 to 2017). We restricted analyses to fish measuring 30 to 69 cm fork length and used a delta modeling approach to quantify species-specific presence-absence and catch-per-unit-effort as a function of survey year, tow location, depth, and bottom temperature. We then calculated an index of spatial overlap across a uniform grid by multiplying standardized predictions of species' abundance. Dietary overlap was calculated across the same uniform grid using Schoener's similarity index. Finally, we assessed the relationship between spatial and dietary overlap as a measure of resource partitioning. We found increases in spatial overlap, moving from east to west in the Gulf of Alaska (eastern: 0.13 ± 0.20; central: 0.21 ± 0.11; western: 0.31 ± 0.13 SD). Dietary overlap was low throughout the study area (0.13 ±

[2] Barnes, CL, Beaudreau AH, Hunsicker ME, and Ciannelli L. 2018. Assessing the potential for competition between Pacific Halibut (*Hippoglossus stenolepis*) and Arrowtooth Flounder (*Atheresthes stomias*) in the Gulf of Alaska. PLoS ONE. 13(12). doi: 10.1371/journal.pone.0209402

0.20 SD). There was no correlation between spatial and dietary overlap, suggesting an absence of resource partitioning along the niche dimensions examined. This finding provides little indication that competition with Arrowtooth Flounder was responsible for changes in Pacific Halibut size-at-age in the Gulf of Alaska; however, it does not rule out competitive interactions that may have affected resource use prior to standardized data collection or at different spatiotemporal scales.

2.2 Introduction

Pacific Halibut (*Hippoglossus stenolepis*) is a large-bodied flatfish that is ecologically important as an apex predator in the Gulf of Alaska [1] and has supported commercial, recreational, and subsistence fisheries for well over a century [2,3]. However, decreases in spawning stock biomass and mean size-at-age between the 1970s and mid-2000s [3–5] have raised concerns among stakeholders and resource managers regarding the long-term productivity of the stock. In fact, declines in size-at-age have been identified as the most important driver of recent trends in stock dynamics for Pacific Halibut, especially in the Gulf of Alaska [6]. Loher [7] described a suite of potentially interacting mechanisms that could be responsible for reduced size-at-age of Pacific Halibut. These included shifts in metabolic demands or efficiencies due to environmental variation, decreases in prey quality or availability, cumulative effects of size-selective fishing, a release of predation pressure on smaller size classes, density-dependent effects due to intraspecific competition, and intensified interspecific competition with Arrowtooth Flounder (*Atheresthes stomias*). Arrowtooth Flounder is a flatfish predator with similar niche requirements that has displayed nearly five-fold increases in biomass over the same time period of observed decreases in halibut size-at-age [8].

A number of studies have been carried out to test the potential mechanisms for decreased Pacific Halibut size-at-age described by Loher [7]. Clark *et al.* [9] found that recent decreases in halibut growth followed a shift in the Pacific Decadal Oscillation between 1976 and 1977, suggesting negative effects of warming temperatures. A subsequent study by Clark and Hare [4] assessed changes in Pacific Halibut size-at-age over a longer timeframe and found relatively small size-at-age in the early 1920s, subsequent increases to a peak around 1970, and decreases to historical size-at-age by the mid to late 1990s. These authors attributed decreases in growth to density dependent effects associated with elevated stock sizes. Recent experiments conducted by Planas [10] have demonstrated positive effects of temperature on somatic growth for captive juveniles. Holsman *et al.* [11] found a similar relationship in the Gulf of Alaska, attributing higher potential growth in juvenile halibut to increased metabolic demands and foraging rates in warmer waters. Prey quality has also been suggested as affecting halibut growth and subsequent size-at-age. For example, Webster [12] found that 'fast' growing halibut (*i.e.*, younger fish from a specific size class) exhibited more benthic-associated diets with prey from higher trophic levels, whereas 'slow' growing halibut (*i.e.*, older fish from the same size class) consumed more, lower trophic-level fishes. Another study by Sullivan [13] used population modeling techniques to test the cumulative effects of size-selective fishing on halibut size-at-age. She found that harvest-based removals explained 30 to 65% of within-regional variation in size-at-age throughout the Gulf of Alaska.

Despite these efforts, our understanding about drivers of change in Pacific Halibut size-at-age is incomplete [3], as many of the alternative hypotheses posed by Loher [7] have not yet been fully explored. This includes the hypothesis that competitive interactions between Pacific Halibut and Arrowtooth Flounder have intensified in the Gulf of Alaska, resulting in

decreased growth rates and subsequent declines in halibut size-at-age. At present, our understanding about this particular mechanism is based on a negative correlation between Pacific Halibut growth and Arrowtooth Flounder biomass [13]. Yet inferring the potential for competition among wild fish populations requires three conditions apart from opposite population trajectories: high spatiotemporal overlap, high dietary overlap, and evidence of resource limitation [14]. These criteria, if met, would suggest that competition is ongoing or is likely to take place in the future. To infer past competition between large-bodied, highly mobile marine species, we employ the theory of resource partitioning, which states that competing species must differentiate their resource use along one or more niche dimensions in order to coexist [*e.g.*, 15–18].

There are three niche dimensions over which species commonly partition resources to alleviate competitive pressures: space, time, and food [18]. In terms of space, individuals may occupy different microhabitats or utilize different depth ranges while foraging on similar prey within the same environment [*e.g.*, 19]. Temporal segregation may take place in the form of occupying the same location at different points in the season or at different times of day [17]. If found in the same place at the same time, competing species must differentiate the types or sizes of prey consumed, a tactic common in marine systems [16–18]. Each of these scenarios reflects an actual niche that is smaller than the virtual (*i.e.*, 'pre-competitive') niche of one or both species [20]. This concept of resource partitioning would be illustrated by a negative relationship between spatiotemporal overlap and dietary overlap at scales relevant to the movements and foraging activities of both potential competitors. In other words, we would expect dietary overlap to decrease with increasing spatiotemporal overlap and vice versa. If a positive relationship between spatiotemporal overlap and dietary

overlap were observed instead, we might infer that competition is in its early stages, is ongoing, or may take place in the future as resources become limiting [14].

We quantified the relationship between spatiotemporal and dietary overlap for Pacific Halibut and Arrowtooth Flounder to assess their degree of resource partitioning along multiple niche dimensions in the Gulf of Alaska using long-term, broad-scale catch and diet data collected by the Alaska Fisheries Science Center (AFSC). Based upon species-specific physiological constraints, we hypothesized that spatial overlap would be greatest at depth and thermal ranges shared by the two species (e.g., 150 to 200 m and 3 to 9 °C) [21–23]. We also expected spatial overlap to be greatest during earlier survey years (*e.g.*, 1996 to 2001), when estimates of Pacific Halibut spawning stock biomass were at their highest [3]. We hypothesized that dietary compositions would be most similar for relatively large (*i.e.*, 60 to 69 cm) size classes of Pacific Halibut and Arrowtooth Flounder, whose diets consist of greater proportions of fish prey [1,24–26]. We also expected dietary overlap to be greatest in the western Gulf of Alaska, where biodiversity is relatively low [21], and vary by year as preferred prey populations fluctuated with changing environmental conditions. Finally, we postulate a negative relationship between spatial overlap and dietary overlap (*i.e.*, evidence of resource partitioning) if competition with Arrowtooth Flounder served as a mechanism for decreased growth and, therefore, size-at-age of Pacific Halibut in the Gulf of Alaska.

2.3 Methods

2.3.1 Overview

We used fishery-independent bottom trawl survey and food habits data collected by the Alaska Fisheries Science Center (AFSC, National Oceanic and Atmospheric Administration;

see [27] for methods) to assess the relationship between spatiotemporal overlap (referred to simply as spatial overlap forward going) and dietary overlap for Pacific Halibut and Arrowtooth Flounder in the Gulf of Alaska. Species-specific distributions and abundances were first modeled as a function of spatiotemporal and environmental covariates. Standardized abundances for each species were then multiplied to derive an index of spatial overlap across a uniform grid system. Dietary overlap was calculated across the same gridded system using an index of similarity that incorporated proportions of prey by weight data. We tested the correlation between spatial and dietary overlap as a measure of resource partitioning. All data analyses were conducted using the statistical programming environment R [28]. Applicable code can be found at: https://github.com/cheryl-barnes/ResourcePartitioning.git.

2.3.2 Data Description

Bottom trawl surveys were carried out by the AFSC's Resource Assessment and Conservation Engineering (RACE) Division using a stratified random sampling design that spanned the International North Pacific Fisheries Commission (INPFC) statistical areas in the Gulf of Alaska (*i.e.*, Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern) [29]. These statistical areas generally correspond to International Pacific Halibut Commission (IPHC) regulatory areas 4A, 3B, 3A, and 2C [30] (Fig 2.1). Surveys were completed triennially from 1990 to 1999 and biennially from 2001 to 2017. However, the Yakutat and Southeastern INPFC areas (IPHC area 2C and the eastern half of 3A) were not surveyed in 2001. Surveys were systematically conducted from west to east, confounding time and space. The Shumagin INPFC area (IPHC area 4A) was typically sampled in mid-May and the Southeastern INPFC area (IPHC area 2C) was typically sampled in mid to late July.

Individual tows were approximately 15 minutes in duration at a continuous vessel speed of 5.6 m per sec [29]. Bottom trawl survey data are publicly available online at https://www.afsc.noaa.gov/RACE/groundfish/survey_data/data.htm.

All fishes were identified to species and enumerated for calculations of catch-per-unit-effort (CPUE; number of fish per hectare) [29]. Capture date, location (latitude and longitude), depth (m), and bottom temperature (°C) were recorded whenever possible. Fork length measurements (cm) were also recorded for up to 200 randomly selected fish per species per haul. Up to five fish lacking any signs of net feeding (*i.e.*, consuming prey items while inside the trawl net) or regurgitation were sampled for diets from each haul and size category: < 31 cm, 31 to 50 cm, 51 to 70 cm, and > 70 cm [30]. Signs of net feeding and regurgitation used to discard samples were the presence of prey in the mouth or gills or a flaccid stomach observed upon dissection. Fish exhibiting signs of regurgitation were discarded and replaced with fish that had non-empty stomachs [31]. Stomach fullness was approximated (1: empty; 2: traces of prey; 3: < 25% full; 4: 25 to 49% full; 5: 50 to 74% full; 6: 75 to 100% full; 7: distended) and prey from non-empty stomachs were identified to the lowest possible taxonomic group, weighed (0.001 g), and measured wherever possible. Food habits data were provided by the AFSC's Resource Ecology and Ecosystem Modeling (REEM) Program for survey years between 1990 and 2013, though fishes caught in the Yakutat INPFC area (eastern half of IPHC area 3A) were not subsampled in 1996, 1999, or 2001 and those caught in the Southeastern INPFC area (IPHC area 2C) were not subsampled prior to 2003. The diet data used in this study are publicly available at https://access.afsc.noaa.gov/REEM/WebDietData/DietDataIntro.php.

2.3.3 Spatial Distributions and Spatial Overlap

We used a multi-stage modeling approach, modified from Hunsicker *et al.* [32] and Shelton *et al.* [33], to quantify spatial overlap between Pacific Halibut and Arrowtooth Flounder in the Gulf of Alaska (Fig 2.2). The smallest fish sampled were predominately Arrowtooth Flounder and the largest individuals were exclusively Pacific Halibut. Because size is another dimension over which resource partitioning can take place [17], we restricted analyses to fish measuring between 30 and 69 cm fork length. Based on available age-length relationships, this restricted size range corresponds to Pacific Halibut ≤ 7 yr [13] and Arrowtooth Flounder ≥ 3 yr [34]. These size restrictions equated to 67.6% of Pacific Halibut and 75.7% of Arrowtooth Flounder subsampled for measurements.

To account for over-dispersion resulting from a zero-inflated data set, we used a delta (*i.e.*, hurdle) model consisting of two parts [35–37]. First, we used generalized additive models (GAMs) with a logit link function to model the binary response of presence (1) or absence (0) as a function of survey year, tow location (*i.e.*, latitude and longitude), depth (m), and bottom temperature (°C) ('mgcv' package in R) [38]. The full model formulation for the probability that species s was present in haul h (assuming a binomial distribution with an expected value of μ) was:

$$log(\mu_{h,s}) = y_i + f_1(\emptyset_h, \lambda_h) + f_2(z_h) + f_3(T_h)$$

$$E(p_{h,s}) = \mu_{h,s}, \quad p_{h,s} \sim B(1, \mu_{h,s}), \quad var(p_{h,s}) \sim \mu_{h,s}(1 - \mu_{h,s})$$

f indicates bivariate (1: longitude $\emptyset$, latitude λ) or univariate (2: depth z and 3: bottom temperature T) smoothing functions and y represents survey year i. Next, we used GAMs with a Gaussian distribution and identity link to model log-transformed CPUE (number of fish per hectare) data, where either Pacific Halibut or Arrowtooth Flounder were present in a haul ('mgcv' package in R) [38]. Log-transformations are commonly used with CPUE data to

reduce skewness resulting from a small number of stations with unusually large catch rates [39]. Because fork lengths were not recorded for all fishes caught, we adjusted haul-specific CPUE estimates by multiplying the proportion of individuals measuring between 30 and 69 cm in subsamples by total CPUE for each haul. Just as with presence-absence, CPUE was modeled as a function of survey year, tow location, depth, and bottom temperature. The full model formulation was: $x_{h,s} = y_i + f_1(\emptyset_h, \lambda_h) + f_2(z_h) + f_3(T_h) + \varepsilon_{h,s}$, where x denotes the natural log of CPUE for species s in haul h.

Separately modeling presence-absence and CPUE for hauls with positive catches [*e.g.*, 40–42] allows for unique responses of species distribution and abundances to model covariates. Though generalized linear mixed models (GLMMs) are more commonly used with the delta modeling approach, we elected for the greater flexibility of GAMs given that species-habitat associations are likely nonlinear [43]. We did not include a spatial autocorrelation term because residuals were not correlated at the scale of our predictions (*i.e.*, 100 km). Though depth and bottom temperature were correlated (r_{8634} = - 0.41, t_{8634} = - 42.08, $p < 0.001$), we were specifically interested in the individual effects of each of these covariates on probability of occurrence and CPUE of Pacific Halibut and Arrowtooth Flounder in the Gulf of Alaska.

To ensure that all GAMs were based on the same suite of data, we excluded tows with missing depths or bottom temperatures. Survey year was treated as a fixed factor and the amount of smoothing for nonparametric terms was determined within each model using generalized cross-validation (GCV) [44]. Smoothing functions for bottom temperature were limited to four knots to avoid over-fitting. However, we did not constrain the degree of smoothing for depth or the bivariate location term (longitude, latitude), enabling detection of patterns in space use that may vary at higher orders. Once full models were constructed,

we used the dredge function from the 'MuMIn' package in R [45] to generate a comprehensive suite of alternative models for each combination of species and response variable (presence-absence and CPUE). We then selected best-fit models using Akaike Information Criterion (AIC), which balances model fit and model complexity [46]. Partial effects of each model covariate were interpreted to help distinguish between environmental drivers of spatial distributions and potential influences of competition.

To calculate spatial overlap from model results, we had to first estimate the probability of occurrence and predicted abundance of Pacific Halibut and Arrowtooth Flounder across a uniform grid system spanning the spatial extent of the bottom trawl survey. This uniform grid allowed for predictions at a finite number of locations (*i.e.*, latitude and longitude coordinates pertaining to individual grid cell centers), established standardized units of area for grouping diet data, and ensured that estimates of spatial and dietary overlap were directly comparable to one another in time and space – a necessary component for assessing the degree of resource partitioning between two potential competitors. We constructed the grid using a Universal Transverse Mercator (UTM) coordinate system before projecting to decimal degrees ('PBSmapping' [47], 'rgdal' [48], 'rgeos' [49], and 'sp' [50] packages in R). Mean depths and mean bottom temperatures for unique combinations of survey year and grid cell were used as input data for estimating probabilities of occurrence and predicted abundances from best-fit GAMs. We then multiplied the probability of occurrence ($PO_{s_{i,j}}$) and predicted abundance ($PA_{s_{i,j}}$) in each survey year i and grid cell j to estimate overall abundance ($A_{s_{i,j}}$) for each species s ($A_{s_{i,j}} = PO_{s_{i,j}} * PA_{s_{i,j}}$). Abundance estimates were standardized by dividing each survey year-grid cell value by the maximum predicted abundance estimate for a given species, across all survey years and grid cells ($std\ A_{s_{i,j}} = A_{s_{i,j}} / \max\ A_s$). We elected to use the species-specific maximum

predicted abundance because it produced the desired range of values (*i.e.*, 0 to 1) for use in calculating spatial overlap. Additionally, standardizing by the species-specific mean or median resulted in nearly identical patterns (though on different scales), demonstrating the robustness of this approach (Fig S2.1). Grid cells resulting in standardized abundances less than 0.25 for both Pacific Halibut and Arrowtooth Flounder suggested poor habitat suitability and were excluded from further analyses. The three grid cells eliminated were among the deepest sampled. Finally, we multiplied standardized abundance estimates to approximate spatial overlap ($S_{i,j}$) between Pacific Halibut (PH) and Arrowtooth Flounder (ATF) throughout the Gulf of Alaska ($S_{i,j} = std\ A_{PH_{i,j}} * std\ A_{ATF_{i,j}}$). Spatial overlap was estimated for 681 unique combinations of survey year and grid cell, with a possible range of values from 0 (no overlap) to 1 (complete overlap).

Year-specific estimates of spatial overlap were averaged within each grid cell to illustrate overall approximations of spatial overlap at each location. We assessed regional and temporal changes in spatial overlap using an analysis of covariance (ANCOVA), treating INPFC statistical area or IPHC regulatory area as the fixed effect and year as the model covariate. Significance was determined using an α set to 0.1. Tukey Honest Significant Differences (Tukey HSD) tests ('stats' package in R [28]) were used to make post hoc comparisons when significant effects of area were identified.

2.3.4 Diet Compositions and Dietary Overlap

As with our spatial modeling, we limited diet analyses to fish measuring 30 to 69 cm fork length. This reduced ontogenetic variation in diet compositions and increased comparability between the two species. These size restrictions equated to 60.2% and 72.2% of the non-empty stomachs sampled for Pacific Halibut and Arrowtooth Flounder, respectively. We

calculated proportions of prey by weight (W) for each prey taxon t found in the stomach of predator species s in survey year i and grid cell j, given the following equation (modified from Chipps and Garvey [51]):

$$W_{t,s,i,j} = \frac{w_{t,s,i,j}}{\sum_{t=1}^{Q} w_{t,s,i,j}}, \text{ where}$$

Q is the total number of prey taxa observed. Proportions were also calculated for distinct size classes (*i.e.*, 30 to 39 cm, 40 to 49 cm, 50 to 59 cm, 60 to 69 cm) to qualitatively assess ontogenetic variation in diets. We elected to calculate proportions of prey by weight instead of some other dietary index (*e.g.*, proportion of prey by number, frequency of occurrence) because we were interested in comparing the relative contributions of various prey taxa to the diets of Pacific Halibut and Arrowtooth Flounder [52]. To provide additional comparisons of dietary niche breadth, we constructed species-specific rarefaction curves (S. Fig 2.10.3.1), computed the Shannon-Weaver index of diversity (H'), and calculated Pielou's index for evenness (J') using the 'vegan' package in R [53].

Schoener's index [54,55] of dietary overlap provides simple and robust calculations that are free from assumptions about the nature of competition [56,57]. Thus, we quantified dietary overlap as follows:

$$D_{i,j} = 1 - \frac{1}{2}\sum_{t}^{Q} |W_{PH_{t,i,j}} - W_{ATF_{t,i,j}}|, \text{ where}$$

W_{PH_t} and W_{ATF_t} are the proportions of prey taxa t (by weight) in the stomachs of Pacific Halibut (PH) and Arrowtooth Flounder (ATF) and Q is the total number of prey taxa observed. Estimates of dietary overlap were calculated across the uniform grid system described for spatial overlap, though grid cells containing fewer than three non-empty stomachs for each predator in a given survey year were excluded. This resulted in estimates of dietary overlap for 123 unique combinations of survey year and grid cell. Like

spatial overlap, the possible range for dietary overlap estimates was between 0 (complete separation) and 1 (complete overlap). Area- and year-specific dietary overlap was quantified as described for spatial overlap.

2.3.5 Resource Partitioning

We used a Pearson's correlation test to quantify the relationship between spatial and dietary overlap for Pacific Halibut and Arrowtooth Flounder in the Gulf of Alaska. Dietary overlap was calculated for fewer grid cells than spatial overlap, therefore cells containing spatial overlap estimates but not dietary overlap estimates were excluded from this analysis. We calculated correlation coefficients and p-values at the basin-wide scale, using all complementary estimates of spatial and dietary overlap. Because sampling effort was spatially variable (*i.e.*, effort was greatest in the western and central areas of the Gulf of Alaska and lowest in the eastern region), we also tested for correlations within each INPFC statistical area and IPHC regulatory area.

2.4 Results

2.4.1 Spatial Distributions

A total of 9,352 survey tows were conducted in the Gulf of Alaska between 1990 and 2017. Of these, 716 were excluded due to missing depth and bottom temperature data. Consequently, 8,636 tows were used to construct species-specific models for presence-absence (Table 2.1). From this subset of tows, 59.1% (5,104) caught Pacific Halibut and 85.9% (7,422) caught Arrowtooth Flounder, and were used to construct species-specific models of CPUE. The majority (n = 422) of excluded tows were because of missing bottom temperatures from the Shumagin INPFC statistical area in 1990.

We identified full GAMs, which accounted for effects of survey year, tow location, depth, and bottom temperature, as the best-fit models for quantifying presence-absence of Pacific Halibut and CPUE of both Pacific Halibut and Arrowtooth Flounder (Table 2.2; Appendices S2.11 and S2.2; S. Table 2.1). Though it is commonplace and can be considered best practice to select the most parsimonious model when ΔAIC is less than two [44], we selected the full model (rather than the one that excluded bottom temperature) for presence-absence of Arrowtooth Flounder. This is because including all model covariates provided consistency for predictions across species and response types (Table 2.2).

Model results for presence-absence indicated that Pacific Halibut and Arrowtooth Flounder were commonly encountered throughout the time series (Appendix S2.1). The likelihood of capturing Pacific Halibut decreased from 1990 to 2001, but generally increased thereafter. With the exception of 1990, Arrowtooth Flounder were nearly always sampled by the bottom trawl. All other variables held constant, Pacific Halibut were most often caught in the western Gulf of Alaska (Shumagin, Chirikof, and Kodiak INPFC areas; IPHC regulatory areas 4A, 3B, and the western half of 3A), at depths shallower than 100 m and in temperatures cooler than 9 °C. Although Arrowtooth Flounder were observed in almost every haul (regardless of geographic location or bottom temperature), encounter rates were greatest at intermediate depths and substantially declined in areas shallower than 100 m or deeper than 450 m (Appendix S2.1).

Model results for CPUE (number per ha) were more variable than those for presence-absence (Appendix S2.2). Though year-to-year variation in CPUE was less than one fish per hectare, Pacific Halibut CPUE generally increased from 1990 to 2017, whereas Arrowtooth Flounder CPUE generally decreased (Appendix S2.2). CPUE for Pacific Halibut was greatest near Unimak Pass (Shumagin area, IPHC regulatory area 4A) and along the

continental shelf-slope break in the eastern region. Arrowtooth Flounder CPUE was greatest in Shelikof Strait (located between Kodiak Island and the Alaska Peninsula) and south to Unimak Island (Shumagin, Chirikof, and Kodiak INPFC areas; IPHC regulatory areas 4A, 3B, and the western half of 3A). Pacific Halibut CPUE peaked at approximately 50 m depth and Arrowtooth Flounder CPUE peaked near 150 m and 350 m. Both species displayed steep declines in CPUE on either side of their respective mode(s). Finally, Pacific Halibut CPUE remained relatively high in waters colder than 9 °C, whereas Arrowtooth CPUE increased with increasing bottom temperature (Appendix S2.1).

Standardized abundance estimates, which combined the probability of occurrence and predicted abundance at a particular time and place, displayed distinct spatial patterns for Pacific Halibut and Arrowtooth Flounder. Standardized abundances for Pacific Halibut were greatest in Cook Inlet, along the east coast of Kodiak Island, and near Unimak Pass, lowest in the central Gulf of Alaska (Kodiak and Yakutat INPFC areas and IPHC area 3A), and moderate to low in the eastern region (Southeastern INPFC area and IPHC area 2C) (Fig 2.3A). Except for Cook Inlet and the deepest areas of the Gulf of Alaska (*i.e.*, the continental shelf-slope break), standardized abundances for Arrowtooth Flounder were relatively high (Fig 2.3B). Grid cell-specific probabilities of occurrence, predicted abundances, and standardized abundance estimates did not vary considerably by survey year.

2.4.2 Spatial Overlap

Overall patterns in spatial overlap (Fig 2.4) between Pacific Halibut and Arrowtooth Flounder closely resembled patterns in Pacific Halibut abundance. Though means ranged from 0.00 (no overlap) to 0.61 (moderate to high overlap) at the survey year-grid cell level,

Pacific Halibut and Arrowtooth Flounder exhibited low spatial overlap (0.26 ± 0.13 SD) at the basin-wide scale. ANCOVA results indicted no significant interaction between survey year and INPFC or IPHC area (INPFC $F_{47,799} = 0.34$ $p > 0.99$; IPHC $F_{34,768} = 0.38$, $p > 0.99$). There were, however, main effects of year (INPFC $F_{12,846} = 11.46$, $p < 0.001$; IPHC $F_{12,802} = 9.26$, $p < 0.01$) and area (INPFC $F_{4,846} = 152.94$, $p < 0.001$; IPHC $F_{3,802} = 145.99$, $p < 0.001$) on spatial overlap. Mean spatial overlap slightly increased throughout the time series and from east to west. Substantial overlap was found along the northeast side of Kodiak Island, the western half of the Alaska Peninsula, and near Unimak Pass. Grid cells with the greatest spatial overlap ($S \geq 0.60$; $n = 2$) measured 31 to 112 m depth and 2.7 to 7.2 °C.

The Tukey HSD test revealed differences in spatial overlap among all area-level combinations except between the Yakutat and Southeastern INPFC statistical areas and between IPHC regulatory areas 4A and 3B. On average, spatial overlap was highest in the Shumagin INPFC statistical area (0.36 ± 0.13 SD) and IPHC regulatory areas 4A and 3B (0.33 ± 0.14 SD) (Fig 2.4). These overlap estimates were followed by Chirikof (0.26 ± 0.12 SD) and Kodiak (0.21 ± 0.11 SD) INPFC statistical areas and IPHC regulatory area 3A (0.19 ± 0.11 SD). The lowest estimate of spatial overlap was found in the eastern Gulf of Alaska (*i.e.*, Yakutat and Southeastern INPFC statistical areas: 0.13 ± 0.08 SD; IPHC regulatory area 2C: 0.10 ± 0.07 SD).

2.4.3 Diet Compositions

Pacific Halibut and Arrowtooth Flounder consumed similar species of prey, though in different proportions. Subsampling for gut content analysis resulted in 1,881 Pacific Halibut stomachs and 5,163 Arrowtooth Flounder stomachs. Of these, 1,488 Pacific Halibut and 2,965 Arrowtooth Flounder contained one or more prey items (Table 2.3). Approximations of

stomach fullness for those sampled with contents indicated that 44.4% of Pacific Halibut and 43.0% of Arrowtooth Flounder stomachs were between half full and distended. When combining all years and areas, both Pacific Halibut and Arrowtooth Flounder consumed 59 different prey taxa. Of these, 47 were common to both predators. Invertebrates and fishes constituted approximately equal proportions by weight of Pacific Halibut diets (fishes = 0.57, invertebrates = 0.43), whereas fishes dominated the diets of Arrowtooth Flounder (fishes = 0.93, invertebrates = 0.07). Generally, Pacific Halibut diets were more diverse (H' = 2.72) and even (J' = 0.58) than diets of Arrowtooth Flounder (H' = 1.72, J' = 0.37; S. Fig 2.2). This was due to the wide variety of invertebrate prey consumed by Pacific Halibut (*e.g.*, crabs and shrimps (49.9%), cephalopods (1.1%), and other benthic invertebrates (1.2%)). Proportions of prey by weight varied by area and size class for both Pacific Halibut and Arrowtooth Flounder (Fig 2.5). For instance, invertebrates were consumed in greater proportions by smaller fish and Pacific Herring (*Clupea pallasii*) made up relatively large proportions of the diets for both predators, but only in the eastern Gulf of Alaska.

2.4.4 Dietary Overlap

Estimates of dietary overlap ranged from 0.00 (no overlap) to 0.81 (high overlap) at the survey year-grid cell level, but the basin-wide mean was considerably low (0.13 ± 0.20 SD; Fig 2.6). We found no significant interactions between survey year and area (ANCOVA: INPFC $F_{23,116} = 0.42$, $p = 0.99$; IPHC $F_{17,120} = 0.35$, $p > 0.99$). There was also no main effect of area on dietary overlap (INPFC $F_{4,139} = 0.59$, $p = 0.67$; IPHC $F_{3,137} = 1.11$, $p = 0.35$). There were, however, differences in dietary overlap with survey year (INPFC: $F_{10,139} = 2.14$, $p = 0.03$, IPHC: $F_{10,137} = 2.57$, $p > 0.01$). Grid cells with the greatest dietary overlap ($D > 0.60$; $n = 9$) measured 134 ± 44 m depth and 5.6 ± 1.2 °C.

2.4.5 Resource Partitioning

Pearson's correlation tests revealed no significant relationship between spatial overlap and dietary overlap for Pacific Halibut and Arrowtooth Flounder in the Gulf of Alaska (Fig 2.7; Fig S2.3). This was true at the basin-wide scale (r_{108} = - 0.02, t_{130} = - 0.20, p = 0.84) and when areas were tested separately. Correlation coefficients for INPFC areas ranged from – 0.02 in Kodiak to 0.37 in Southeastern. Correlation coefficients for IPHC areas ranged from – 0.06 in 3B to 0.72 in 2C (all p-values > 0.1).

2.5 Discussion

Pacific Halibut and Arrowtooth Flounder distributions and abundances varied as a function of survey year, location (*i.e.*, latitude and longitude), depth, and bottom temperature. However, year, location, and temperature had much less of an effect on shaping Arrowtooth Flounder distributions. Given the ubiquity of Arrowtooth Flounder in the Gulf of Alaska, we found that patterns in spatial overlap were largely driven by the distributions and abundances of Pacific Halibut. We found support for the hypothesis that spatial overlap between Pacific Halibut and Arrowtooth Flounder would be greatest at intermediate depths (73 to 90 m) and temperatures (2.7 to 8.3 °C). Contrary to our expectations, spatial overlap did not vary substantially by year and was not at its greatest during periods of high halibut spawning stock biomass. Diet compositions were most similar for the larger (*i.e.*, 30 to 69 cm) size classes analyzed in this study, as anticipated. Sparse stomach sampling in both time and space led to relatively few unique combinations of survey year and grid cell, thus we were unable to make strong inferences about spatiotemporal patterns in dietary overlap. Estimates of dietary overlap were generally low throughout the study area, despite our hypothesis that low species diversity in the western

Gulf of Alaska would lead to greater overlap in the diets of Pacific Halibut and Arrowtooth Flounder. Finally, resource partitioning between Pacific Halibut and Arrowtooth Flounder was not apparent in the Gulf of Alaska given that there was no correlation between spatial overlap and dietary overlap at the scale of our analyses.

2.5.1 Spatial Distributions and Spatial Overlap

Pacific Halibut were most often encountered in the relatively cold (< 5 °C), shallow (< 100 m) waters of the western Gulf of Alaska. Observed distributions for the size range of halibut assessed reflect known movement patterns, with smaller individuals more frequently occupying the western Gulf of Alaska before emigrating eastward [58]. However, relatively high densities of Pacific Halibut in the western Gulf of Alaska may also be confounded with the survey design, which consistently moves from west to east as the summer progresses [29]. This is because temporary aggregations of prey may be found in the western Gulf of Alaska at the time of data collection due to localized increases in primary productivity in late spring [59].

Arrowtooth Flounder were observed in virtually every survey year and tow location, demonstrating a wide spatial niche breadth in the Gulf of Alaska. The greatest catch rates for Arrowtooth Flounder were in moderately deep (200 to 300 m) waters of Shelikof Strait. Though Arrowtooth Flounder were encountered in similar frequencies regardless of temperature, CPUE increased in warmer waters. The relationship between Arrowtooth Flounder abundance and temperature is corroborated by observations made in the Eastern Bering Sea, where Arrowtooth Flounder prefer warmer waters and actively avoid the “cold pool” (*i.e.*, temperatures < 2 °C) [23,60].

Because Arrowtooth Flounder were so ubiquitous throughout the Gulf of Alaska, patterns in spatial overlap were primarily driven by distributions of Pacific Halibut. The only major exception was in the shallow (< 100 m) waters of Cook Inlet, where relatively few Arrowtooth Flounder were found. The western Gulf of Alaska, which is characterized by a broader continental shelf, greater amounts of shallow water (< 200 m) habitat, and colder (< 5 °C) bottom temperatures resulted in higher spatial overlap than the eastern Gulf of Alaska, which is characterized by a relatively narrow continental shelf and warmer (> 5 °C) bottom temperatures. Additionally, moderate to high estimates of spatial overlap may be attributable to the greater productivity, higher groundfish densities, and lower overall species diversity in the western Gulf of Alaska [21,59]. At the finer grid cell level, there was a wide range of spatial overlap values with few high estimates suggesting more localized species-specific responses to exogenous factors. However, we cannot distinguish whether estimates of spatial overlap result from competitive interactions or some other variable (*e.g.*, habitat suitability, prey availability) using only species' distributions and abundances. Therefore, we evaluated the linear relationship between spatial overlap and dietary overlap to provide insight into the role of competition as a plausible driver of observed patterns of resource partitioning.

2.5.2 Diet Compositions and Dietary Overlap

We found that diet compositions of Pacific Halibut were more diverse and benthically associated than Arrowtooth Flounder. This is comparable to findings from previous studies, which have shown a) wider varieties of fish and invertebrates consumed by Pacific Halibut and b) that crabs constitute greater proportions of prey by weight in diets of small Pacific Halibut, whereas Walleye Pollock (*Gadus chalcogrammus*) dominate the diets of similarly

sized Arrowtooth Flounder [11,24,25,27,61]. Diet compositions of Pacific Halibut and Arrowtooth Flounder were more similar at larger sizes due to the greater proportions of fish consumed by Pacific Halibut. Although a relatively wide dietary niche likely provides Pacific Halibut with greater flexibility in responding to fluctuating community compositions and nearby competitors [20], prey switching may have metabolic consequences (*e.g.*, decreased growth [11]). This is especially true if that shift is directed from higher quality, energy dense prey to lower quality taxa, as inferred from differences in diets between fast- and slow-growing halibut [11,12]. However, interpreting changes in diet compositions is context-dependent and requires information about prey availability and predator preferences.

Given differences in diet compositions, we found dietary overlap between Pacific Halibut and Arrowtooth Flounder to be low, but highly variable throughout the Gulf of Alaska. Mean dietary overlap was greatest in a single grid cell in the eastern Gulf of Alaska, where more Pacific Herring (*Clupea pallasii*) were consumed by both species. The increased proportions of herring in the diets of Pacific Halibut and Arrowtooth Flounder sampled from Southeast Alaska, specifically in 2005, coincided with relatively high herring biomass during late summer [62]. This particular grid cell is also located in close proximity to a herring spawning stock boundary designated by the Alaska Department of Fish and Game [62]. Feeding on locally abundant prey is evidence of the opportunistic nature of these predators, which likely exhibit prey switching in response to prey populations.

A necessary caveat when comparing the diets of Pacific Halibut and Arrowtooth Flounder is that stomach fullness and diet compositions may, in part, reflect differential responses to capture and handling. Arrowtooth Flounder are relatively soft-bodied fish that tend to regurgitate more frequently when disturbed [31, Barnes, pers. obs.]. This

physiological stress response could be responsible for the greater proportion (approximately 2.5 times) of empty stomachs for Arrowtooth Flounder when compared to Pacific Halibut [24]. Though fish displaying signs of regurgitation were excluded as part of the sampling protocol [26], it is difficult to know for certain whether or not partial regurgitation occurred before fish made it to the sampling table. Additionally, discarding fish suspected of regurgitation could bias sampling toward fish with partially full or empty stomachs [31] and away from those feeding most heavily, as fish with the fullest stomachs may be prone to regurgitation.

2.5.3 Resource Partitioning and the Potential for Competition

Niche-based competition theory states that the coexistence of competing species is only possible through resource partitioning, which differentiates the ecological requirements of species to prevent competitive exclusion [16,20,63). Despite opposing trajectories of Pacific Halibut growth and Arrowtooth Flounder biomass at the basin-wide scale [13], we did not detect resource partitioning (*i.e.*, a negative relationship between spatial overlap and dietary overlap) as would be expected if competition was ongoing or had taken place in the recent past. With low (eastern Gulf of Alaska) to moderate (western and central Gulf of Alaska) overlap in space and generally low overlap in diet, it is possible that the two species require different enough resources to preclude competition (*i.e.*, overlap estimates reflect the virtual niche of each species rather than actual niche breadths that had been constricted due to competition). If this were the case, bottom-up processes would be responsible for variation in capture probability, relative abundance, diet composition, and niche overlap. For example, the niche breadth of Pacific Halibut might be restricted to shallower waters, cooler temperatures, and invertebrate prey regardless of whether or not Arrowtooth Flounder

occupy deeper depths and warmer waters or more heavily rely on fish as prey (or vice versa; Appendices S2.1 and S2.2). Given historically low size-at-age of Pacific Halibut [4], it is also plausible that disparate responses to environmental change (*e.g.*, recruitment) are responsible for recent changes in the population trajectories of Pacific Halibut (decreasing) and Arrowtooth Flounder (increasing) [14]. Notably, however, a lack of evidence for resource partitioning may also be due to a divergence in resource use prior to the collection of necessary data. Though fishery catch data and various survey data are available prior to the most recent declines in Pacific Halibut size-at-age [*e.g.*, 4,8], a lack of standardized methods and sparse diet information prevent an analysis of resource partitioning before 1990.

Several factors could have impacted our ability to assess resource partitioning between Pacific Halibut and Arrowtooth Flounder. One reason we may have been unable to detect a relationship between spatial and dietary overlap is a low signal to noise ratio. When tracking paired means for spatial and dietary overlap through time, there appeared to be a negative correlation, especially from 2001 onward (Fig 2.7). With a few exceptions, where there was no change in spatial overlap from one survey year to the next, an increase in the mean overlap along one dimension corresponded with a decrease in the mean overlap for the other. However, confidence intervals indicated that 1999, 2003, and 2005 were the only survey years to yield statistically distinct estimates of spatial and dietary overlap, making the detection of any pattern (should one exist) impossible at the basin-wide scale. This low signal to noise ratio persisted at finer (*i.e.*, INPFC and IPHC area) spatial scales, though the degree of habitat heterogeneity encompassed by statistical or regulatory areas likely continues to mask interactions at this scale. Sample size limitations and a need to aggregate diet data precluded an assessment of patterns in resource use at scales finer

than the uniform 100 km x 100 km grid cell, which still may be too broad to detect ecologically relevant interactions between the two species.

Effectively characterizing the resource use of marine fishes, especially those with opportunistic foraging strategies, requires a large number of samples (ideally ≥ 50 observations per grouping) [64]. Low sample sizes generally increase variation in diet compositions, make it difficult to detect patterns in consumption of prey, and can result in underestimations of niche overlap [65]. Interestingly, the number of moderate to high estimates of dietary overlap ($D \geq 0.40$) appeared to increase with sample size. The spatiotemporal coverage of dietary overlap estimates was sparse in part because we required at least three non-empty Pacific Halibut and Arrowtooth Flounder stomachs in each combination of survey year and grid cell. Robust estimates of diet composition are especially important, given that trophic separation is more common than spatial separation in marine systems [18,66]. As such, increased sampling for gut content analysis would enhance our understanding about the relationships between spatial and dietary overlap and whether or not competition can serve as a mechanism for changes in size-at-age. Specifically increasing sampling effort in the Yakutat and Southeastern INPFC areas (IPHC areas 3A and 2C) and more consistent sampling through time should increase the power to detect relationships in niche overlap, should they exist. However, more robust estimates of diet composition and higher spatiotemporal resolution of the dietary overlap measure may fail to improve inferences about competition using the theory of resource partitioning. This is because prey that are relatively rare in the diets of Arrowtooth Flounder could undergo local depletion as a result of high Arrowtooth Flounder abundance. If that particular prey taxon is important for Pacific Halibut, intense competitive pressure may persist even in cases of low dietary overlap, regardless of the degree of spatial overlap between the two predators.

The apparent lack of resource partitioning may have also been an artifact of selecting specific size classes for analyses. We selected similar fork lengths as our basis for comparison across species because body size has been identified as more important than phylogeny in determining functional roles within a particular food web [67]. Larger individuals are often considered superior competitors because of their increased visual acuity, faster swimming speeds, and more aggressive behaviors [68]. However, smaller species can have negative effects on larger species by consuming shared prey at one or more life stage. A tractable example of these interactions has been described for the small but abundant Redside Shiner (*Richardsonius balteatus*) and relatively large Rainbow Trout (*Salmo gairdneri*) in British Columbia [*e.g.*, 69–71]. Due to their increased population sizes and widespread distributions, shiners were able to overgraze amphipods before they attained sizes available to juvenile trout. This resulted in a need for juvenile trout to feed on suboptimal prey, thereby reducing their growth rates at early stages. Based on the differences in diet compositions and rates of piscivory for Pacific Halibut and Arrowtooth Flounder, it is possible that some other combination of size (*e.g.*, 20 to 29 cm Arrowtooth Flounder and 60 to 69 cm Pacific Halibut) is more appropriate to assess resource partitioning and infer competition between the two species. In fact, Yang [24] found that dietary overlap was highest for Arrowtooth Flounder ≥ 40 cm and Pacific Halibut ≥ 80 cm. However, we lacked sufficient data to restrict size ranges in this way.

Finally, we may have been unable to detect resource partitioning because of numerous, interacting drivers of halibut size-at-age. If competition between Pacific Halibut and Arrowtooth Flounder was at least in part responsible for declines in halibut size-at-age, its effects could have been moderated by various impacts from environmental variation [11,31,72] or masked by other ecological interactions such intensified intraspecific

competition during periods of high Pacific Halibut biomass [*e.g.*, 73]. Consequences of size-selective fishing (as identified by Sullivan [13]) within the size ranges analyzed for this study, however, should be minimal. In short, we have necessarily used simple models with a set of *a priori* assumptions to study one component of a highly complex ecological system, thereby increasing the likelihood of interpretive error [74]. Additionally, any identified mechanism would not explain an observed pattern at all spatial or temporal scales [75,76]. Continued data collection would enhance our understanding about changing niche requirements of Pacific Halibut and Arrowtooth Flounder and how interactions between the two species may vary in time, space, and under different environmental conditions. Standardized surveys that focused on a few dominant groundfish prey (*e.g.*, various crabs, pollock, and herring) would also provide context for interpreting spatiotemporal changes in niche overlap [17,77,78]. It would also be valuable to collect age information pertaining to fish subsampled for gut content analysis. At present, randomly-sampled fish are used to estimate age compositions of the catch from bottom trawl surveys and these ages are not linked to individual stomach samples. If these data were available, spatial models and diet analyses could be stratified by age in addition to length. Age information would also enable direct associations between diet compositions and size-at-age, which would be especially useful for future studies. A reassessment of resource partitioning would also be useful in the near-term, given a recent stabilization of Pacific Halibut size-at-age [3] and considerable reductions in Arrowtooth Flounder biomass [8].

2.5.4 Implications for Fisheries Management

Our results are limited to the time frame of data collection, areas sampled, and sizes of fish analyzed. As such, conclusions presented herein can only be applied to resource use

by Pacific Halibut and Arrowtooth Flounder measuring 30 to 69 cm in the Gulf of Alaska since 1990. Data were unavailable to assess resource use in non-summer months or simultaneously in all areas throughout the summer. Due to ontogenetic shifts and known seasonal migrations, spatial distributions and diet compositions are likely different for other size and age classes of fish as well as in different seasons (*i.e.*, fall, winter, or spring). Despite these limitations, our study represents a first step toward evaluating the hypothesis that intensified competition with an increasing Arrowtooth Flounder population has contributed to decreases in mean size-at-age of Pacific Halibut in the Gulf of Alaska.

Changing community compositions is not unique to the Gulf of Alaska and spatiotemporal variation in life history is not unique to Pacific Halibut. There have been increases in the frequency of "native invasions" and "biotic homogenization" resulting from new niche opportunities associated with climate change [79,80]. Additionally, a number of other species (*e.g.*, Pacific salmon, *Oncorhynchus* spp.; [81–83]) have experienced changes in size-at-age, suggesting an effect of shared environmental drivers on fish growth. Given such variations in size-at-age, there is considerable value in understanding how shifts in the abundance of one species may impact life history traits of other species that are connected through their use of space or position in the food web.

We found regional patterns in spatial overlap for Pacific Halibut and Arrowtooth Flounder, with higher overlap in the western Gulf of Alaska and lower overlap in the eastern Gulf of Alaska. Declines in halibut size-at-age were also greatest in the western Gulf of Alaska when compared to lower, though highly variable, declines in the east [13,84]. A number of other studies have suggested west-east patterns in the Gulf of Alaska. Holsman *et al.* [11] found increased metabolic demands and increased foraging rates for juvenile halibut in the western and central Gulf of Alaska. More generally, Mueter and Norcross [21]

found that the western Gulf of Alaska displayed greater groundfish abundances, but lower species richness and diversity than the eastern Gulf of Alaska. These clear differences in community compositions and physiological processes between east and west provide support for the spatially-explicit assessment models currently in development for Pacific Halibut, Arrowtooth Flounder, and other groundfish predators in the Gulf of Alaska [*e.g.*, 85,86]. Incorporating spatial structure into stock assessments and fishery management plans will likely enhance our understanding about the ecological mechanisms responsible for changes in population abundance (*e.g.*, localized adaptation, ontogenetic changes in habitat use, trophic interactions, density-dependent effects, structural changes related to fishing) [43]. It will also help us understand how components of a particular community respond to environmental cues (*e.g.*, temperature and salinity), enabling better predictions of ecological change [87]. More broadly, results from this study improve our understanding about complex ecological interactions among economically important groundfish species at various scales and contribute to our existing knowledge about how these interactions may change in time, space, and under different environmental conditions.

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2.8 Figures

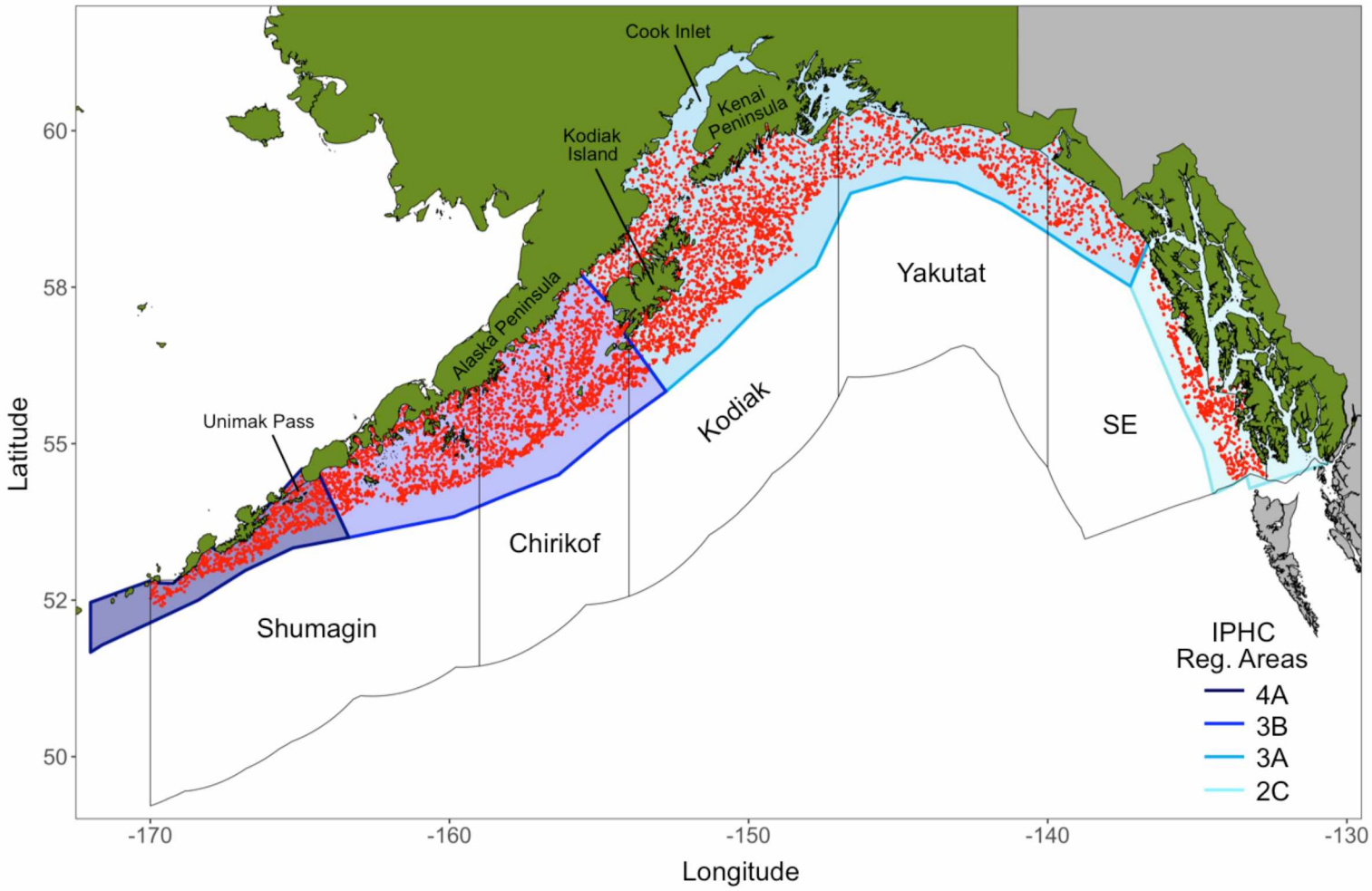


Fig 2.1 Map of bottom trawl survey area (Alaska Fisheries Science Center, NOAA; 1990 to 2017). Red dots indicate individual tow locations throughout the Gulf of Alaska. Unfilled polygons outlined in black denote Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern (SE) statistical areas defined by International North Pacific Fisheries Commission (INPFC). Blue-shaded polygons illustrate International Pacific Halibut Commission (IPHC) regulatory areas 4A, 3B, 3A, and 2C.

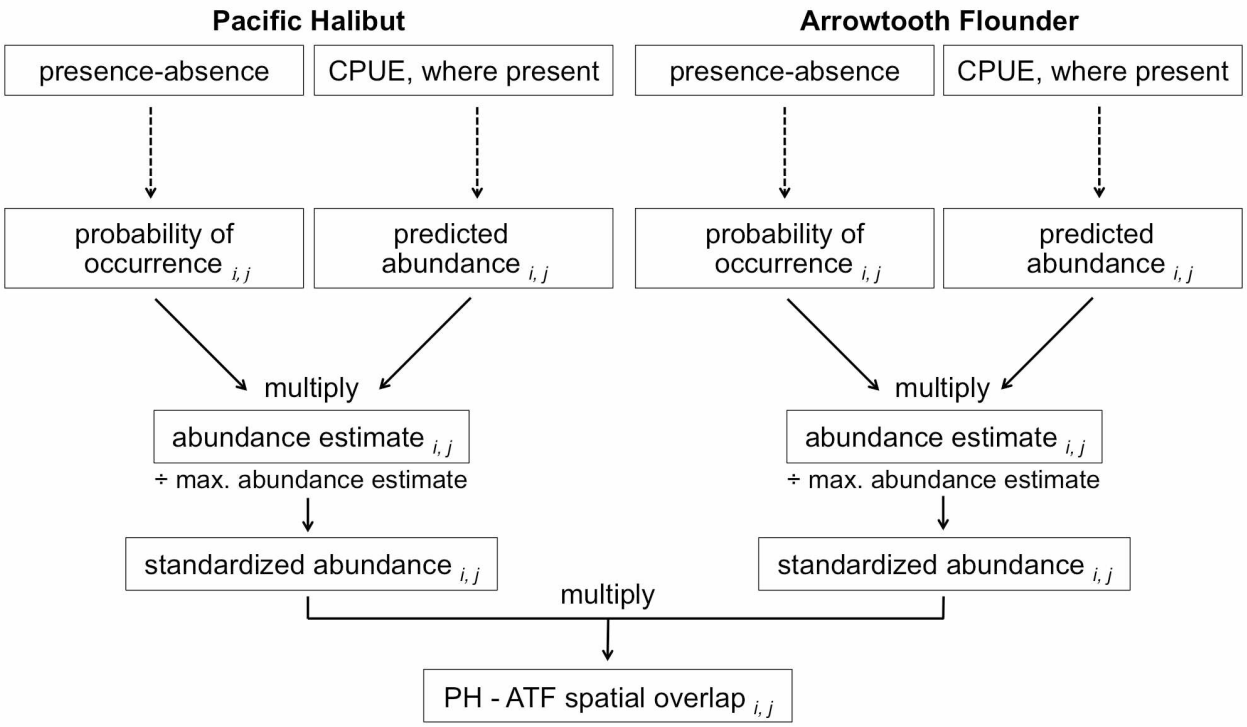


Fig 2.2 Analytical framework used to quantify spatial overlap between Pacific Halibut and Arrowtooth Flounder. First, bottom trawl survey data from the Gulf of Alaska and generalized additive models were used to separately quantify presence-absence and catch-per-unit-effort (CPUE; number per ha) as a function of survey year, tow location (latitude, longitude), depth, and bottom temperature. Model results were used to estimate the probability of occurrence and predicted abundance for Pacific Halibut or Arrowtooth Flounder in each combination of survey year i and uniform grid cell j. These predictions were multiplied to estimate abundance, which was then standardized by dividing each survey year-grid cell value by that species' maximum across all years. Finally, standardized abundances for Pacific Halibut and Arrowtooth Flounder were multiplied to approximate spatial overlap in each survey year and grid cell. Analytical methods were modified from those described by Hunsicker *et al.* [32] and Shelton *et al.* [33].

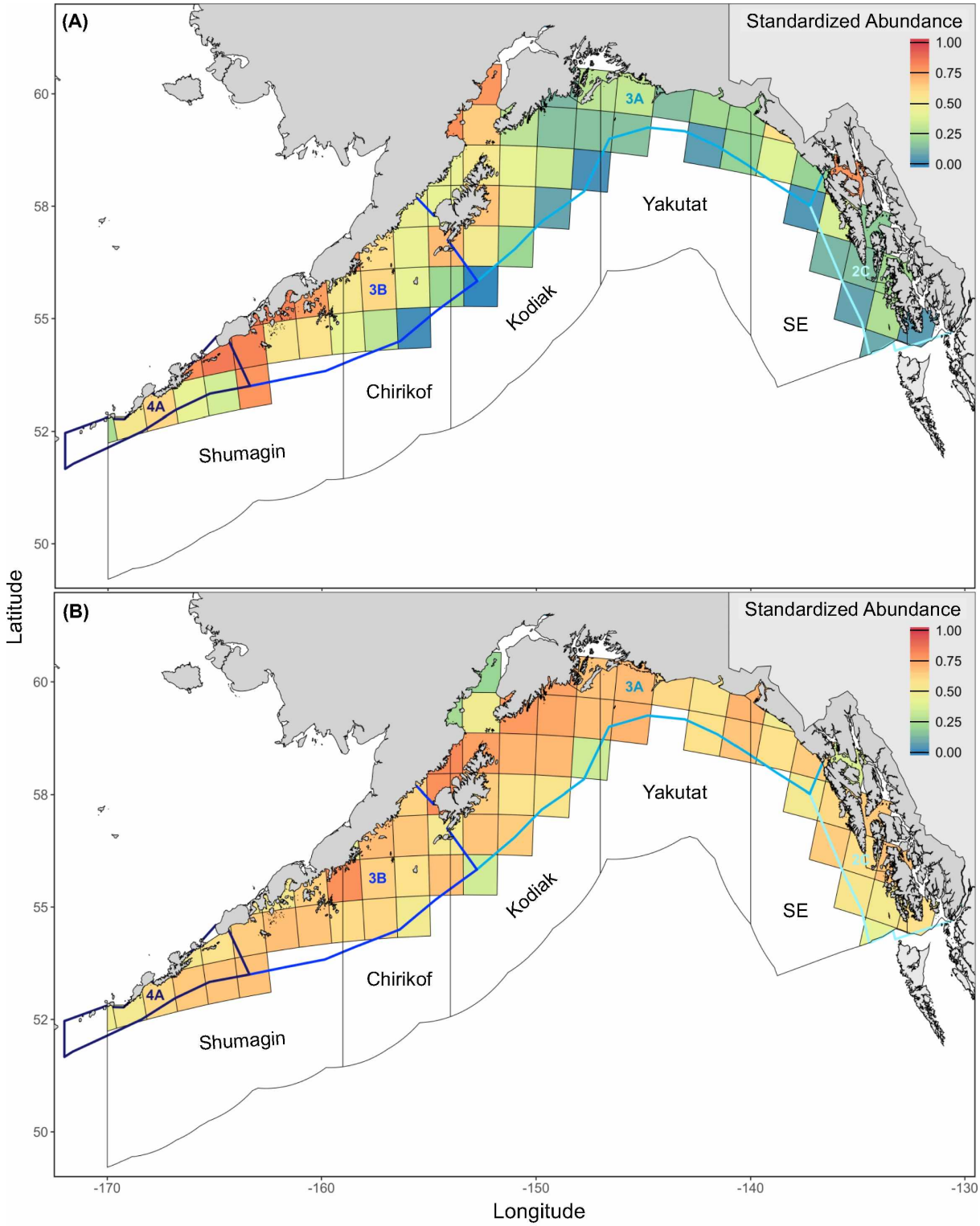


Fig 2.3 Mean standardized abundances for (A) Pacific Halibut and (B) Arrowtooth Flounder (1990 to 2017). Filled squares represent individual 100 km x 100 km grid cell estimates. Polygons denote International North Pacific Fisheries Commission (INPFC) statistical areas (black outlines) and International Pacific Halibut Commission (IPHC) regulatory areas (blue-shaded outlines) in the Gulf of Alaska.

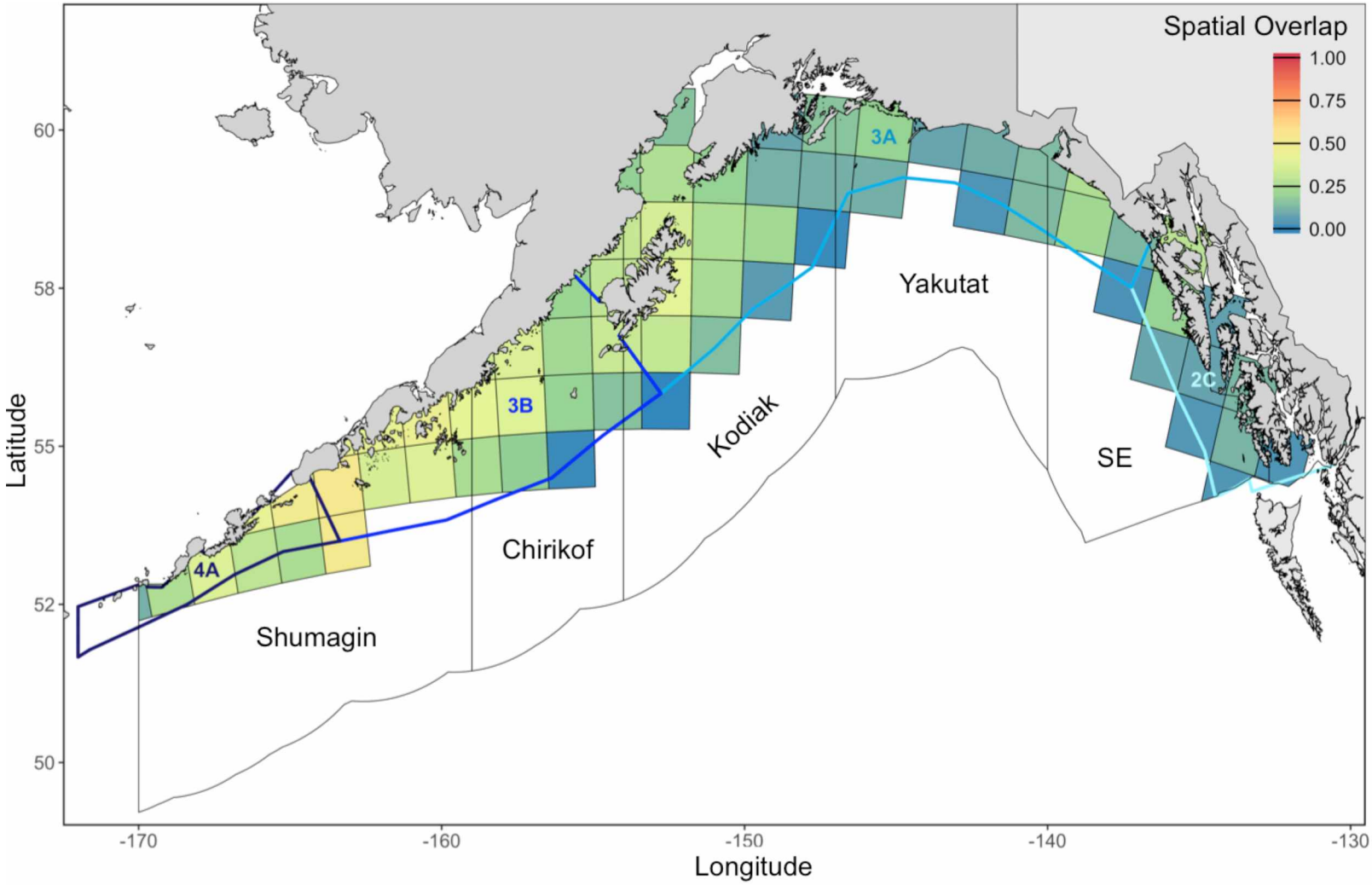


Fig 2.4 Mean spatial overlap between Pacific Halibut and Arrowtooth Flounder (1990 to 2017). Filled squares represent individual 100 km x 100 km grid cell estimates. Polygons denote International North Pacific Fisheries Commission (INPFC) statistical areas (black outlines) and International Pacific Halibut Commission (IPHC) regulatory areas (blue-shaded outlines) in the Gulf of Alaska.

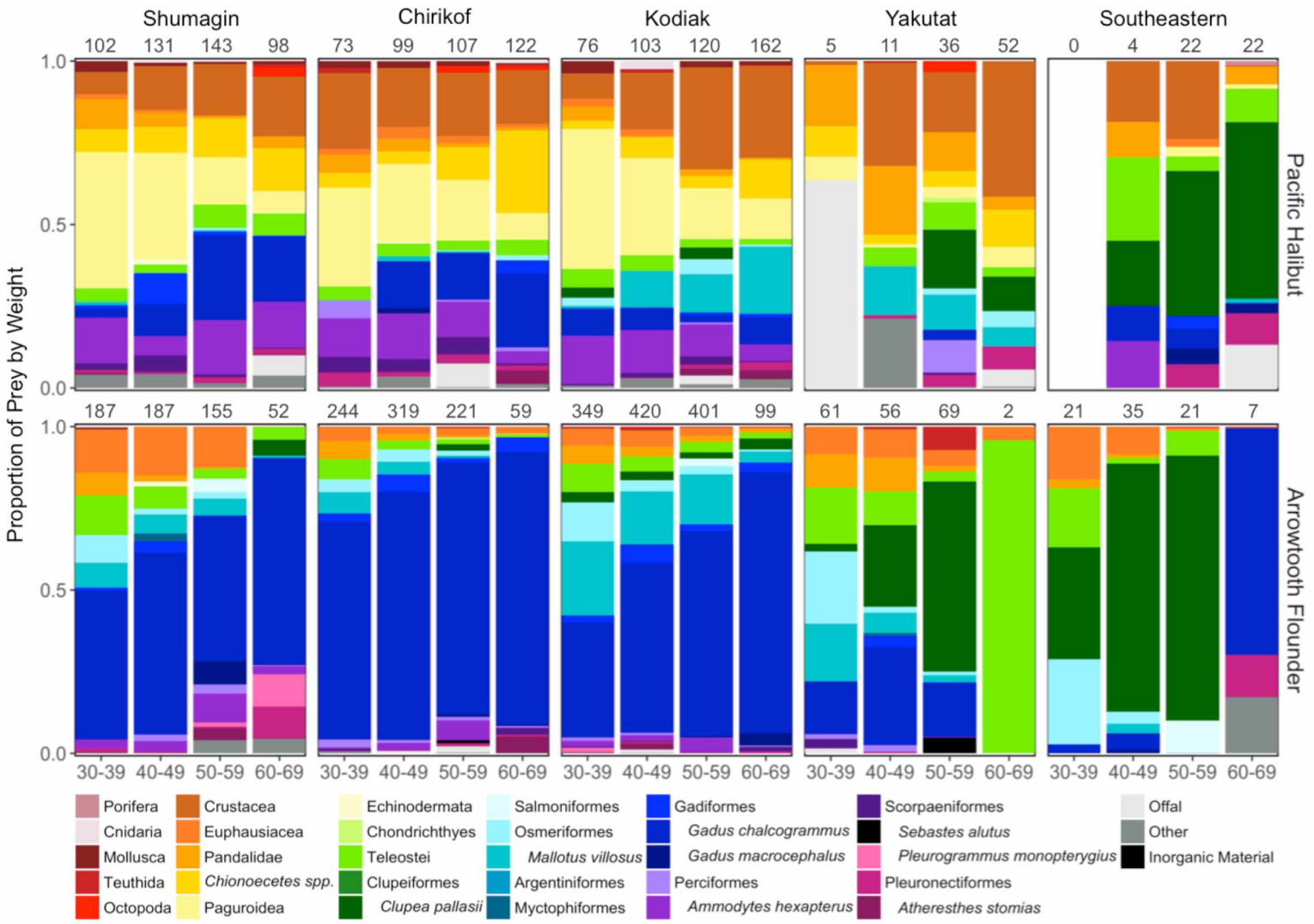


Fig 2.5 Mean proportions of prey by weight for Pacific Halibut and Arrowtooth Flounder (all survey stations, 1990 to 2013). Calculations were grouped by International North Pacific Fisheries Commission (INPFC) statistical area and size class. Sample sizes are indicated above each stacked bar. Prey taxa that constituted less than 0.01 by weight were classified into broader taxonomic groups (*e.g.*, phyla for invertebrate taxa and order for fishes).

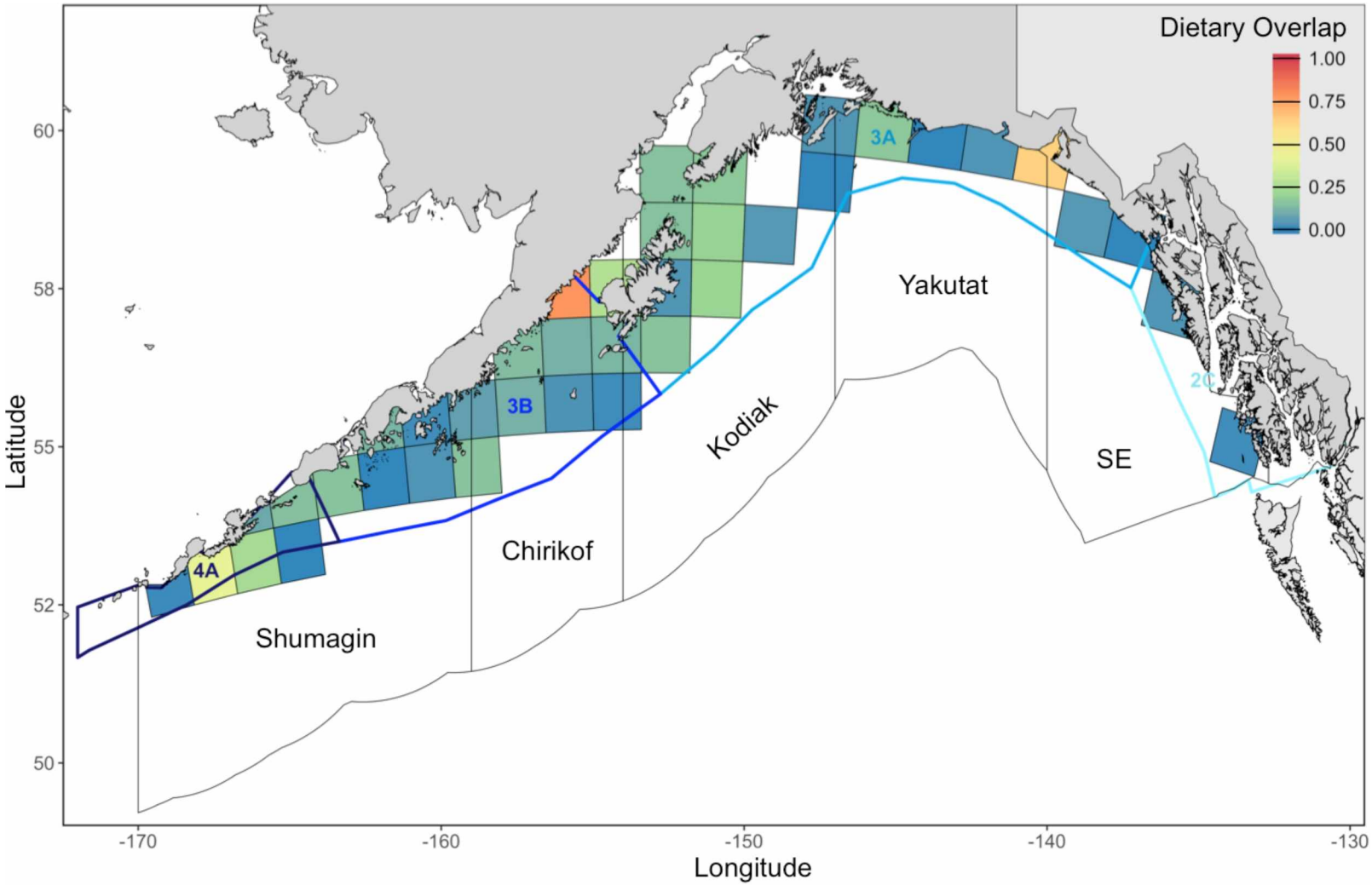


Fig 2.6 Mean dietary overlap between Pacific Halibut and Arrowtooth Flounder (1990 to 2013). Filled squares represent individual 100 km x 100 km grid cell estimates. Polygons denote International North Pacific Fisheries Commission (INPFC) statistical areas (black outlines) and International Pacific Halibut Commission (IPHC) regulatory areas (blue-shaded outlines) in the Gulf of Alaska.

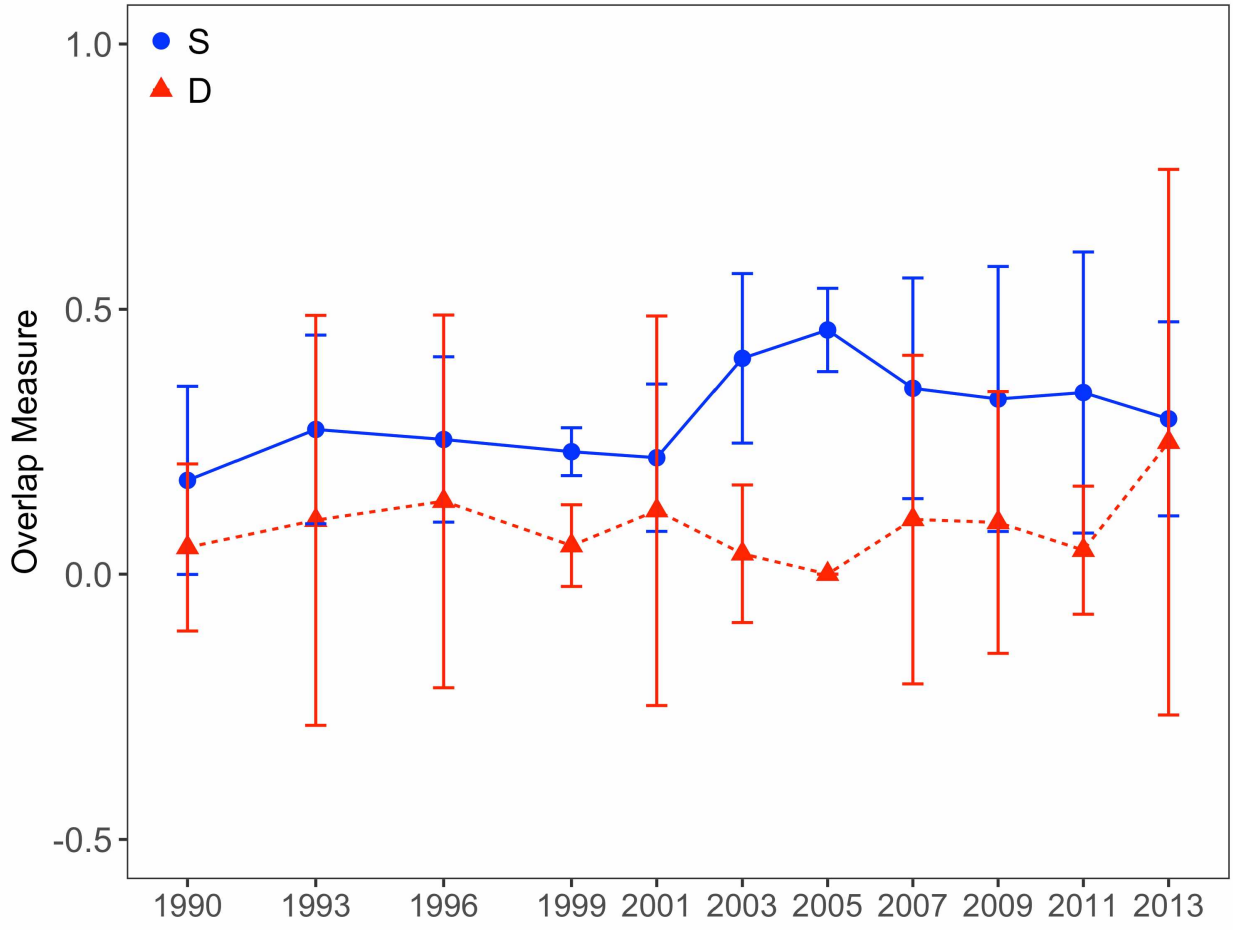


Fig 2.7 Niche overlap estimates for Pacific Halibut and Arrowtooth Flounder in the Gulf of Alaska (1990 to 2013). Spatial overlap (S) is denoted by blue circles and solid lines. Dietary overlap (D) is denoted by red triangles and dashed lines. Error bars represent 95% confidence intervals.

2.9 Tables

Table 2.1 Number of tows that captured fish measuring 30 to 69 cm fork length. Numbers of Pacific Halibut (A) or Arrowtooth Flounder (B) are shown by International North Pacific Fisheries Commission (INPFC) statistical area and survey year. The total numbers of tows conducted are shown in parentheses. Only tows with complete environmental data were tabulated.

A. Pacific Halibut: 5,104 (8,636)

INPFC Area	1990	1993	1996	1999	2001	2003	2005	2007	2009	2011	2013	2015	2017
Shumagin	5	144	124	118	111	186	142	172	169	146	115	136	104
1,672 (2,029)	(5)	(166)	(169)	(143)	(136)	(229)	(176)	(205)	(196)	(162)	(136)	(182)	(124)
Chirikof	16	98	100	79	75	107	103	138	134	109	94	133	77
1,263 (1,955)	(25)	(168)	(168)	(161)	(133)	(170)	(174)	(196)	(186)	(155)	(126)	(175)	(118)
Kodiak	32	124	68	112	86	137	146	151	145	145	114	193	115
1,568 (2,809)	(78)	(210)	(186)	(242)	(189)	(242)	(287)	(257)	(275)	(226)	(187)	(252)	(178)
Yakutat	35	46	27	53	0	26	29	21	37	25	25	37	29
390 (1,056)	(117)	(117)	(105)	(132)	(76)	(0)	(90)	(57)	(83)	(68)	(61)	(80)	(70)
Southeastern	2	4	25	15	0	22	31	20	19	22	9	25	17
211 (787)	(61)	(65)	(88)	(64)	(0)	(78)	(92)	(64)	(72)	(54)	(38)	(66)	(45)
Total	90	416	344	377	272	478	451	502	504	447	357	524	342
	(286)	(726)	(716)	(742)	(458)	(795)	(819)	(779)	(812)	(665)	(548)	(755)	(535)

B. Arrowtooth Flounder: 7,422 (8,636)

INPFC Area	1990	1993	1996	1999	2001	2003	2005	2007	2009	2011	2013	2015	2017
Shumagin	4	142	148	137	103	208	170	190	180	153	116	158	114
1,823 (2,029)	(5)	(166)	(169)	(143)	(136)	(229)	(176)	(205)	(196)	(162)	(136)	(182)	(124)
Chirikof	18	144	142	142	108	139	150	152	163	137	107	144	106
1,652 (1,955)	(25)	(168)	(168)	(161)	(133)	(170)	(174)	(196)	(186)	(155)	(126)	(175)	(118)
Kodiak	62	183	167	202	157	203	258	213	241	204	162	221	166
2,439 (2,809)	(78)	(210)	(186)	(242)	(189)	(242)	(287)	(257)	(275)	(226)	(187)	(252)	(178)
Yakutat	57	98	98	115	0	70	80	50	77	64	58	78	63
908 (1,056)	(117)	(117)	(105)	(132)	(76)	(0)	(90)	(57)	(83)	(68)	(61)	(80)	(70)
Southeastern	23	27	72	50	0	64	77	53	64	45	34	54	37
600 (787)	(61)	(65)	(88)	(64)	(0)	(78)	(92)	(64)	(72)	(54)	(38)	(66)	(45)
Total	164	594	627	646	368	684	735	658	725	603	477	655	486
	(286)	(726)	(716)	(742)	(458)	(795)	(819)	(779)	(812)	(665)	(548)	(755)	(535)

Table 2.2 Results for the top three models, by species and response type (presence-absence, CPUE, where present). X indicates the variables (survey year, longitude and latitude, depth [m], bottom temperature [°C]) included in each alternative model. The deviance explained (Dev., %), degrees of freedom (df), log likelihood (logLik), ΔAIC, Akaike weight (W_i), and generalized cross validation (GCV) score are also noted. The selected model for each case is shown in bold.

	Variables Included in Alt. Model									
Model	Year	Lon, Lat	Depth	Temp	Dev. (%)	df	logLik	ΔAIC	W_i	GCV
Pacific Halibut										
Presence-absence	**X**	**X**	**X**	**X**	**45.6**	**48**	**- 3179**	**0.0**	**0.997**	**- 0.253**
	X	X	X		45.4	44	- 3188	11.5	0.003	- 0.251
		X	X	X	43.9	35	- 3279	174.1	0.000	- 0.232
CPUE, where present	**X**	**X**	**X**	**X**	**46.4**	**52**	**- 7120**	**0.0**	**1.000**	**0.973**
	X	X	X		46.2	49	- 7132	17.7	0.000	0.967
		X	X	X	44.7	40	- 7199	133.5	0.000	0.999
Arrowtooth Flounder										
Presence-absence	X	X	X		40.1	49	- 2099	0.0	0.637	- 0.503
	X	**X**	**X**	**X**	**40.2**	**50**	**- 2098**	**1.1**	**0.363**	**- 0.503**
		X	X	X	33.1	38	- 2347	474.6	0.000	- 0.448
CPUE, where present	**X**	**X**	**X**	**X**	**40.3**	**53**	**- 12745**	**0.0**	**1.00**	**1.842**
	X	X	X		40.0	50	- 12764	33.4	0.00	1.850
		X	X	X	39.0	41	- 12827	140.6	0.00	1.877

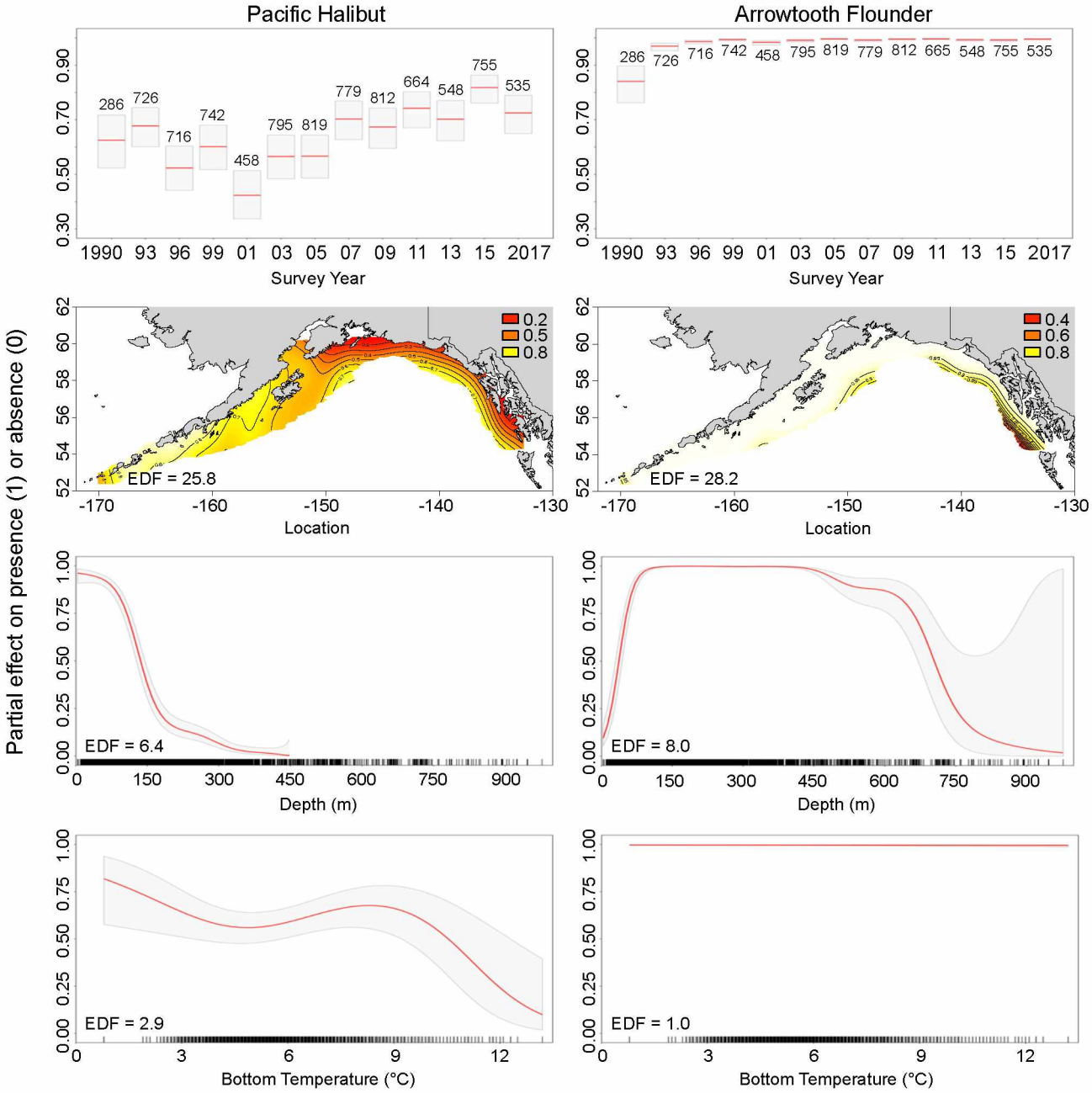
Table 2.3 Number of non-empty stomachs sampled, by International North Pacific Fishery Commission (INPFC) statistical area and survey year. Numbers for Pacific Halibut are listed as the top line in each category and Arrowtooth Flounder are shown below. Food habits data were not yet available for 2015 or 2017.

INPFC Area	1990	1993	1996	1999	2001	2003	2005	2007	2009	2011	2013	Total
Shumagin	15	50	31	3	98	26	13	55	37	43	103	474
	18	21	138	25	85	49	11	44	55	56	79	581
Chirikof	28	42	22	0	79	31	7	16	44	36	96	401
	106	87	219	58	135	44	16	35	43	43	57	843
	143	111	244	94	280	42	26	34	74	97	124	1,269
Yakutat	2	9	0	0	0	3	7	17	14	17	35	104
	14	28	1	0	0	10	15	19	39	23	39	188
Southeastern	0	0	0	0	0	0	4	11	10	7	16	48
	0	0	0	0	0	5	12	15	25	13	14	84
Total	84	123	83	40	252	69	32	157	145	151	352	1,488
	281	247	602	177	500	150	80	147	236	232	313	2,965

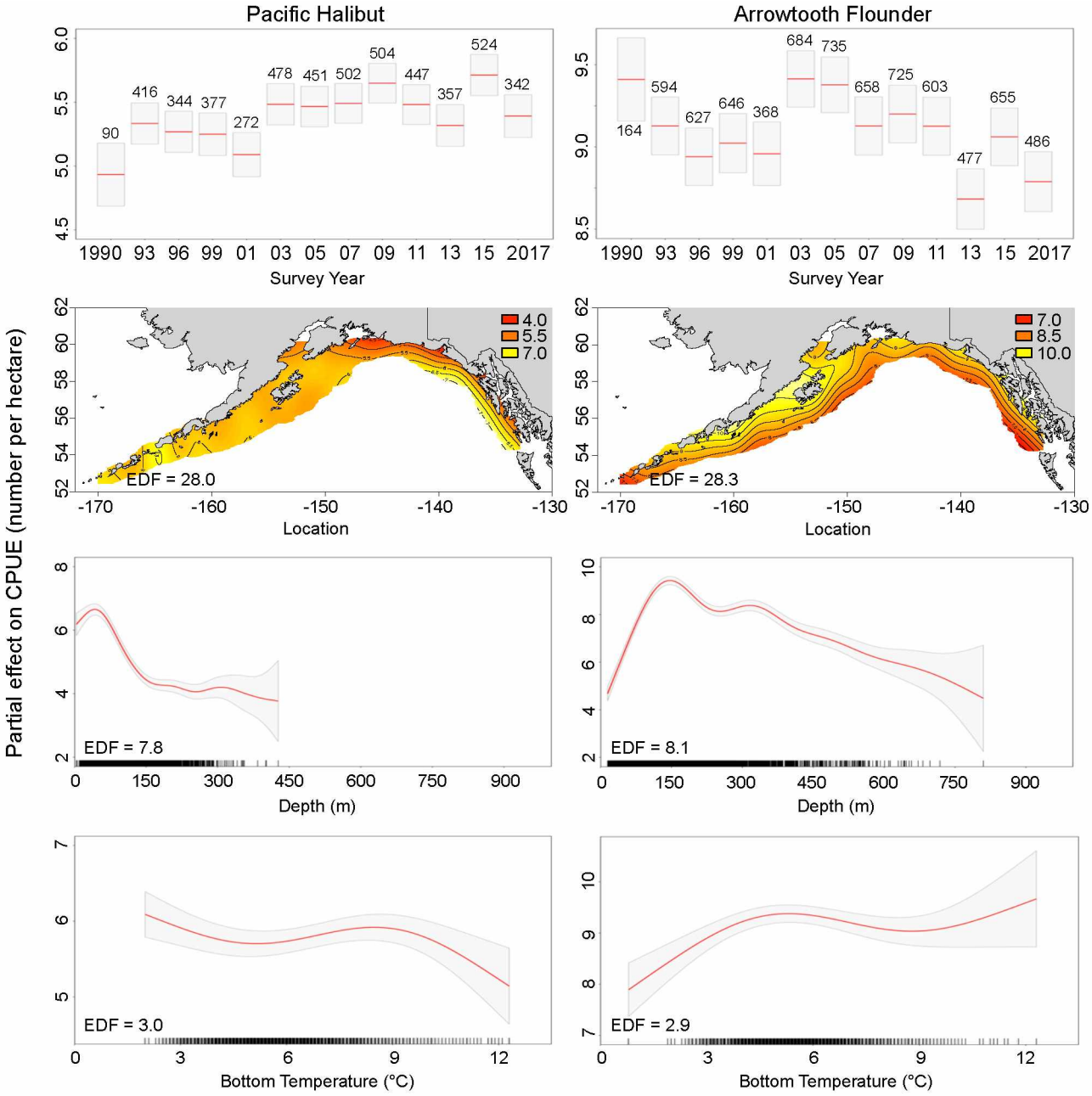
2.10 Supporting Information

2.10.1 Supplemental Appendices

Appendix S2.1 Partial effects of model covariates on presence (1) or absence (0) of Pacific Halibut (left) and Arrowtooth Flounder (right) in the Gulf of Alaska (1990 to 2017). Plots were produced using 'visreg' [88] and 'mgcv' [38] functions in R. Red lines illustrate predicted relationships from generalized additive models (GAMs) and gray bands denote 95% confidence intervals. Numbers above or below survey years denote sample sizes (*i.e.*, the number of hauls conducted). Effective degrees of freedom (EDF) and individual data points (black ticks along x-axis) are shown for smoothed univariate covariates.



Appendix S2.2 Partial effects of model covariates on catch-per-unit-effort (CPUE; number per ha) for Pacific Halibut (left) and Arrowtooth Flounder (right) in the Gulf of Alaska (1990 to 2017). Plots were produced using 'visreg' [88] and 'mgcv' [38] packages in R. Red lines illustrate predicted relationships from generalized additive models (GAMs) and gray bands denote 95% confidence intervals. Numbers above or below survey years denote sample sizes (*i.e.*, the number of hauls conducted). Effective degrees of freedom (EDF) and individual data points (black ticks along x-axis) are shown for smoothed univariate covariates.



2.10.2 Supplemental Figures

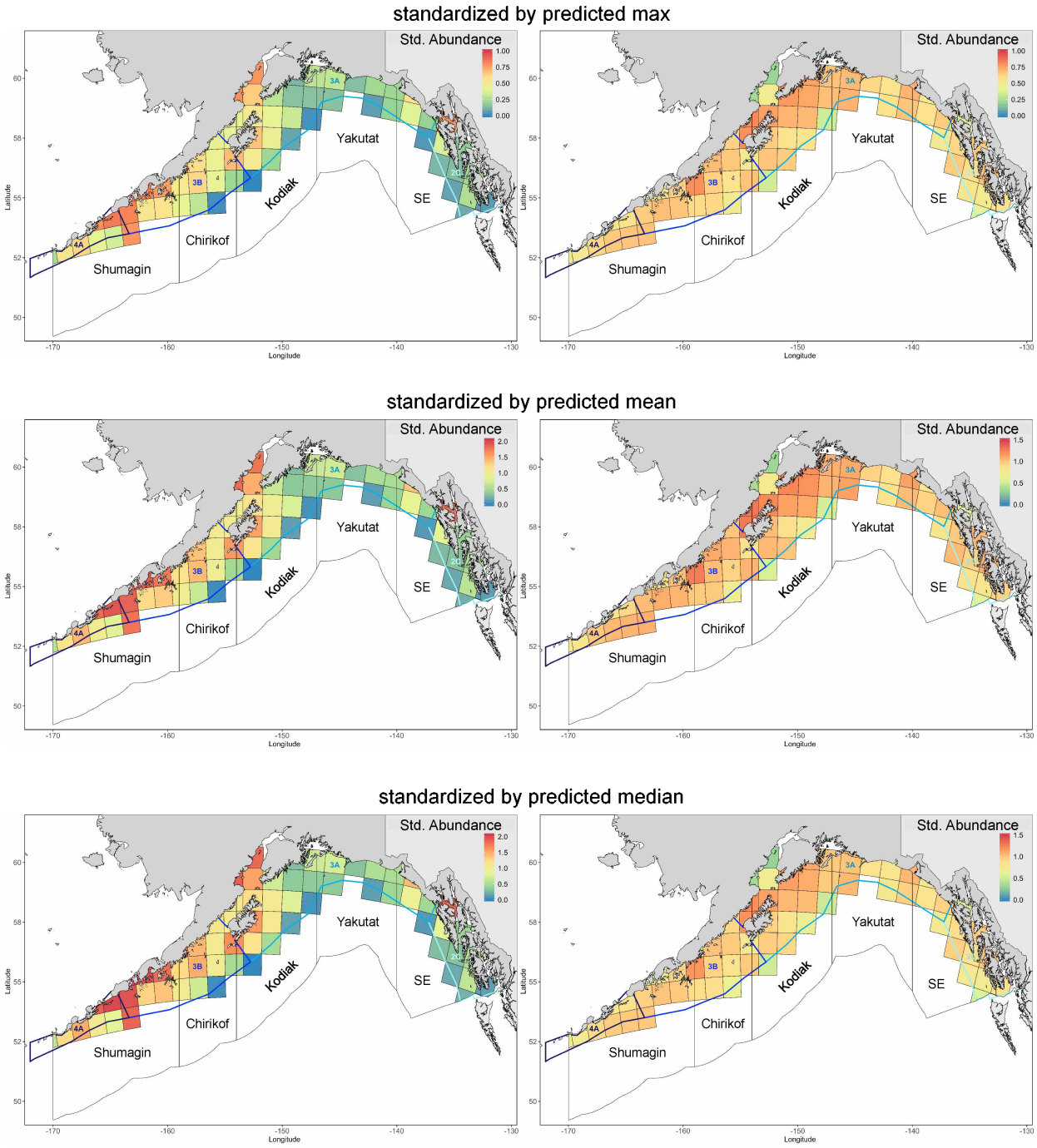


Fig S2.1 Mean grid cell-specific estimates of abundance (1990 to 2017) for Pacific Halibut (left) and Arrowtooth Flounder (right) using different standardization methods (*i.e.*, dividing individual grid cell abundances by the species-specific maximum, mean, or median predicted abundance).

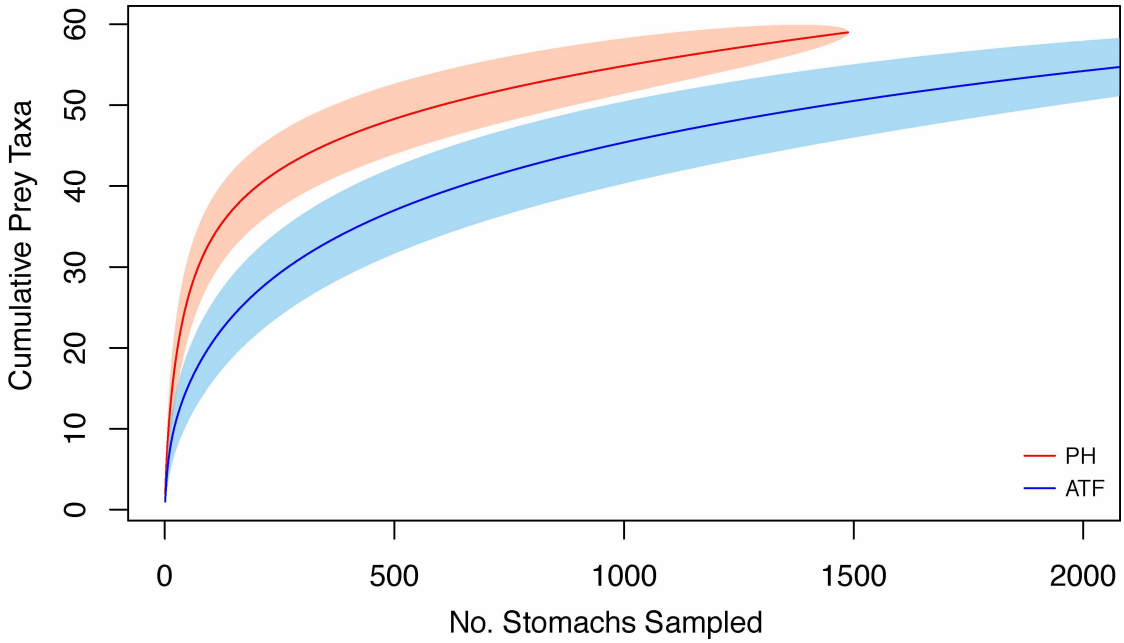


Fig S2.2 Rarefaction curves illustrating changes in number of cumulative prey taxa encountered with sample size. Pacific Halibut is shown in red and Arrowtooth Flounder is shown in blue. Shaded areas indicate 95% confidence intervals.

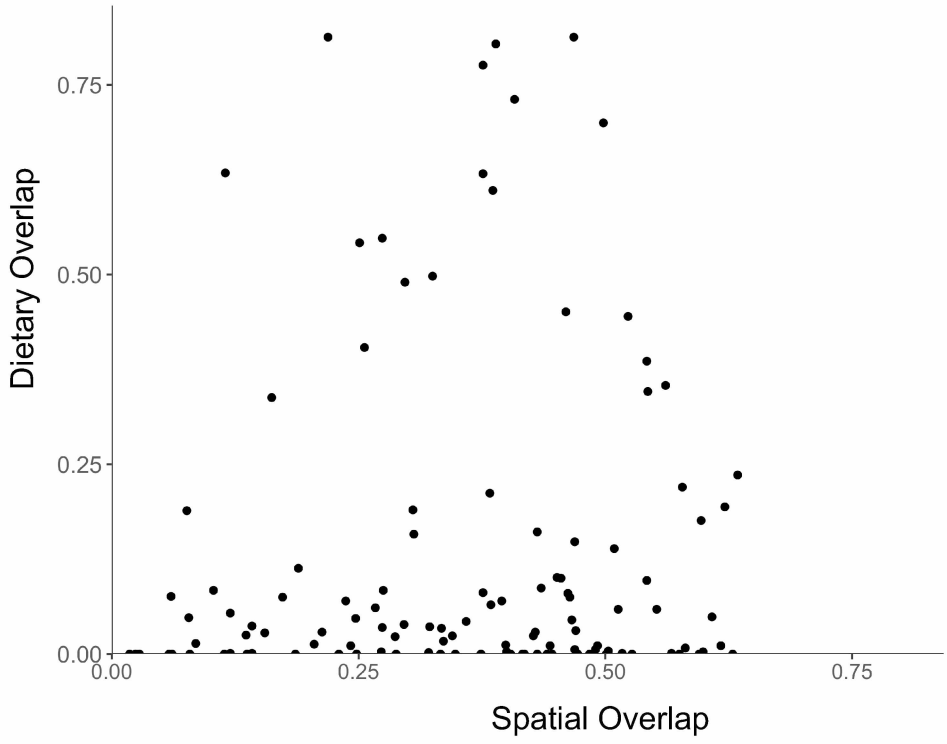


Fig S2.3 Relationship between spatial overlap and dietary overlap for Pacific Halibut and Arrowtooth Flounder in the Gulf of Alaska (1990 to 2013). Each data point represents a unique combination of survey year and grid cell.

2.10.3 Supplemental Tables

Table S2.1 Parameter estimates from selected generalized additive models for Pacific Halibut (A) and Arrowtooth Flounder (B). Because year was treated as a factor, 1990 is denoted as the model intercept and estimates for subsequent years are shown as differences from 1990. Smoothed variables include location (latitude, longitude), depth, and bottom temperature. Non-significant terms ($\alpha = 0.1$) are grayed out.

A. Pacific Halibut

Selected GAM	Estimate	Std. Error	z- or t-value	edf	Chi Sq. or F	p-value	Adj. R^2 (scale est.)
Presence / Absence							0.514 (1.000)
(intercept)	- 0.158	4.273	- 0.04			0.971	
1993	0.229	0.192	1.19			0.233	
1996	- 0.419	0.193	- 2.17			0.030	
1999	- 0.100	0.196	- 0.51			0.608	
2001	- 0.821	0.215	- 3.81			< 0.001	
2003	- 0.248	0.196	- 1.26			0.206	
2005	- 0.244	0.192	- 1.27			0.205	
2007	0.350	0.199	1.76			0.079	
2009	0.212	0.197	1.08			0.281	
2011	0.545	0.200	2.73			0.006	
2013	0.346	0.206	1.68			0.093	
2015	0.990	0.198	5.00			< 0.001	
2017	0.458	0.205	2.24			0.025	
Lon, Lat				25.8	346.4	< 0.001	
Depth				6.4	1123.3	< 0.001	
Bottom Temp				2.9	15.7	0.0031	
CPUE (no. per ha)							0.459 (0.963)
(intercept)	4.931	0.106	46.64			< 0.001	
1993	0.401	0.116	3.45			< 0.001	
1996	0.336	0.119	2.83			0.005	
1999	0.317	0.119	2.66			0.008	
2001	0.157	0.123	1.28			0.201	
2003	0.551	0.117	4.73			< 0.001	
2005	0.534	0.116	4.61			< 0.001	
2007	0.558	0.117	4.79			< 0.001	
2009	0.716	0.117	6.14			< 0.001	
2011	0.549	0.116	4.73			< 0.001	
2013	0.385	0.118	3.26			0.001	
2015	0.780	0.115	6.77			< 0.001	
2017	0.459	0.118	3.88			< 0.001	
Lon, Lat				26.0	12.4	< 0.001	
Depth				7.8	210.8	< 0.001	
Bottom Temp				3.0	7.8	< 0.001	

Table S2.1 (cont) Parameter estimates from selected generalized additive models for Pacific Halibut (A) and Arrowtooth Flounder (B). Because year was treated as a factor, 1990 is denoted as the model intercept and estimates for subsequent years are shown as differences from 1990. Smoothed variables include location (latitude, longitude), depth, and bottom temperature. Non-significant terms (α = 0.1) are grayed out.

B. Arrowtooth Flounder

Selected GAM	Estimate	Std. Error	z- or t-value	edf	Chi Sq. or F	p-value	Adj. R^2 (scale est.)
Presence / Absence							0.383 (1.000)
(intercept)	0.039	0.160	0.24			0.808	
1993	1.811	0.202	8.97			< 0.001	
1996	2.604	0.214	12.15			< 0.001	
1999	3.351	0.231	14.48			< 0.001	
2001	2.431	0.234	10.37			< 0.001	
2003	3.041	0.215	14.14			< 0.001	
2005	3.930	0.231	17.01			< 0.001	
2007	3.065	0.223	13.73			< 0.001	
2009	3.694	0.234	15.77			< 0.001	
2011	3.904	0.244	15.97			< 0.001	
2013	3.231	0.237	13.64			< 0.001	
2015	3.195	0.226	14.12			< 0.001	
2017	3.756	0.257	14.62			< 0.001	
Lon, Lat				28.3	574.3	< 0.001	
Depth				8.0	1113.3	< 0.001	
Bottom Temp				1.0	1.1	0.294	
CPUE (no. per ha)							0.399 (1.829)
(intercept)	7.896	0.107	73.75			< 0.001	
1993	- 0.283	0.120	- 2.35			0.019	
1996	- 0.470	0.120	- 3.93			< 0.001	
1999	- 0.388	0.120	- 3.22			0.001	
2001	- 0.452	0.129	- 3.49			< 0.001	
2003	0.003	0.120	0.03			0.978	
2005	- 0.033	0.118	- 0.28			0.782	
2007	- 0.283	0.121	- 2.34			0.019	
2009	- 0.211	0.120	- 1.76			0.079	
2011	- 0.285	0.121	- 2.35			0.019	
2013	- 0.728	0.124	- 5.86			< 0.001	
2015	- 0.349	0.121	- 2.90			0.004	
2017	- 0.622	0.124	- 5.03			< 0.001	
Lon, Lat				28.3	48.7	< 0.001	
Depth				8.1	299.7	< 0.001	
Bottom Temp				2.9	12.2	< 0.001	

Chapter 3 Size and trophic niche separation between two groundfish predators in nearshore Southeast Alaska [3]

3.1 Abstract

Competition is among the most important ecological interactions affecting top predators. To minimize effects of competition, these animals must partition resources along one or more niche dimensions. Trophic niche separation (*i.e.,* dissimilarity in diet compositions) among spatially overlapping individuals is the principal strategy for resource partitioning among marine fishes. Trophic niche separation is often assessed by comparing diet compositions of fishes with similar body sizes. However, differences in allometric growth among co-occurring flatfishes suggests that size-dependent gape limitation varies among species. We quantified relationships between fork length and gape dimensions (height and width) for two potentially competing flatfish predators, Pacific Halibut (*Hippoglossus stenolepis*) and Arrowtooth Flounder (*Atheresthes stomias*). We then compared length- and gape-specific diets to better understand the effect of each metric on trophic niche partitioning. We worked with fishing lodge captains and private recreational anglers to collect morphometric (N_{ATF} = 594, N_{PH} = 1430) and diet data (N_{ATF} = 169, N_{ATF} = 920 [stomachs with prey]) for Arrowtooth Flounder and Pacific Halibut in nearshore Southeast Alaska (2015 and 2016). Overlap in size distributions according to gape width (mm) was three times greater than overlap by fork length (cm). We found species-specific differences in diet compositions by gape width, but not fork length or gape height. Generally, Pacific Halibut diets were more diverse and benthically-associated than those of Arrowtooth Flounder. Despite these differences, we estimated similar trophic levels and moderate to

[3] Barnes CB, Beaudreau AH, and Yamada RN. In Prep. Size and trophic niche separation between two groundfish predators in nearshore Southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences. Forthcoming.

high dietary overlap for all size classes and metrics, except for the largest gape widths. Pacific Herring (*Clupea pallasii*) and pollock/cod (*Gadus* spp.) were important prey for both predators. The greatest differences in diets were driven by taxa-specific contribution of invertebrate prey. Positive relationships between prey size and predator size suggested gape limitation within the size range of Pacific Halibut sampled. Our results highlight the importance of considering gape as a metric of size when assessing niche partitioning among large-bodied fishes, given differences in allometric growth. For Pacific Halibut and Arrowtooth Flounder, substantial dietary overlap suggested greater potential for competition among smaller individuals. Partitioning of prey at larger gape sizes indicates a possible mediation of competitive effects with ontogeny. Although Pacific Halibut possess many qualities of a superior competitor (*e.g.,* larger maximum body sizes, stronger musculature, larger eyes), Arrowtooth Flounder may have a competitive advantage at smaller body sizes, given relatively large gapes and an earlier onset of piscivory.

3.2 Introduction

Competition is a major driving force of natural selection (Diamond 1978; Schoener 1982). Its negative effects range from decreased growth to competitive exclusion – both resulting from a shrunken niche breadth of one or more competitors (Schoener 1974). Two species must therefore limit their ecological similarity along one or more resource dimensions if they are to coexist (MacArthur and Levins 1967; Colwell and Futuyama 1971; May 1974; Pianka 1974). Among the ways in which organisms can partition resources, dietary separation has been identified as most important in marine systems (Ross 1986; Piet *et al.* 1998). Increased mobility and habitat heterogeneity in nearshore environments allow fish and other animals to move among microhabitats while foraging, thus facilitating

the partitioning of prey over space (Schoener 1974; Ross 1986). Additionally, divergent feeding morphologies are common in aquatic communities and promote trophic niche separation through specialized foraging (Keast and Webb 1966; Stoner and Livingston 1984; Swanson *et al.* 2003).

Size provides an avenue for partitioning prey among closely related taxa with similar morphologies (Roughgarden 1976; Ross 1986). This dimension is especially important in determining resource use by large, piscivorous fishes that experience numerous shifts in diet throughout their ontogeny (Piet *et al.* 1998; Garrison and Link 2000). As these fish grow, faster swimming speeds and better visual acuity lead to increased foraging efficiency (Keast and Webb 1966; Webb 1976; Beamish 1978; Blaxter 1986). For these reasons, food web ecologists often use fork lengths as a basis for comparing diets among different fish species (*e.g.,* Zahn Seegert *et al.* 2014; Ustups *et al.* 2016; Rohan and Buckley 2018). Gape measurements also impact the range of prey types and sizes consumed (Scharf *et al.* 2000), but are frequently unaccounted for when estimating dietary overlap. Because gape limitation is an important driver of trophic niche breadth (*e.g.*, Schmitt and Holbrook 1984; Piet *et al.* 1998; Russo *et al.* 2008), gape size should be considered when comparing diets among sympatric fishes. Ideally, multiple metrics of size would be employed during food habits studies because differing allometric relationships (*e.g.,* Schake *et al.* 2014; Dunic and Baum 2017; Mihalitsis and Bellwood 2017) and disparate effects of length and gape may influence our interpretations of resource partitioning and subsequent inferences about interspecific competition.

Flatfishes (order: Pleuronectiformes) represent a monophyletic group that is ideal for studying resource partitioning. Taxa within this group exhibit high morphological similarity that promotes the use of benthic habitats (Munroe 2005; Gibson *et al.* 2005). Piscivorous

flatfishes share a number of physical characteristics unique to that feeding guild, which include relatively large body sizes and jaw structures that are well-adapted for consuming larger, faster, stronger prey (Link *et al.* 2005). Differences in head structure and gape size have been identified as the most important mechanism for trophic diversification among flatfishes given their markedly similar body morphologies and habitat utilizations (*e.g.,* Piet *et al.* 1998; Russo *et al.* 2008). Within morphological constraints, flatfishes tend to opportunistically consume prey according to their local abundances (Link *et al.* 2005). However, dietary separation resulting from subtle differences in morphology (among species or ontogenetically within a species) remains the primary way in which functionally similar flatfishes partition resources and minimize competition (*e.g.,* Carter *et al.* 1991; Amara *et al.* 2001; Sigurd Høines and Bergstad 2002; Guedes and Araújo 2008; Schückel *et al.* 2011).

Arrowtooth Flounder (*Atheresthes stomias*) and Pacific Halibut (*Hippoglossus stenolepis*) are examples of closely related, morphologically similar flatfishes that occupy the same general habitats during similar timeframes. Given their functional similarity and spatiotemporal overlap, we would expect some degree of resource partitioning to allow for their coexistence. Overlapping niche breadths, along with decreased Pacific Halibut size-at-age (Clark *et al.* 1999) and concurrent increases in Arrowtooth Flounder biomass (Spies *et al*. 2017), led to the hypothesis that competition may be important in the Gulf of Alaska (Loher 2013). A previous study that estimated the relationship between spatial overlap and dietary overlap for Pacific Halibut and Arrowtooth Flounder found no evidence of resource partitioning among fishes with similar fork lengths (Barnes *et al.* 2018). However, apparent species-specific differences in gape size at the same body length suggested that other size-based metrics of resource partitioning should be examined. Although Pacific Halibut can

grow to be much larger (267 cm and 363 kg) than Arrowtooth Flounder (84 cm and 8.6 kg), the two groundfish predators have several prey in common (Yang 1995; Yang and Nelson 1999). With relatively high dietary overlap between Arrowtooth Flounder ≥ 40 cm and Pacific Halibut ≥ 80 cm fork length, Yang (1995) theorized that gape size should have the greatest effect on prey compositions of Arrowtooth Flounder and Pacific Halibut.

We collected morphometric and diet data to assess effects of body size and gape size on diet compositions, trophic levels, and niche breadth of Arrowtooth Flounder and Pacific Halibut in Southeast Alaska. Generally, we were interested in understanding whether fine-scale patterns in resource use (*i.e.,* site-specific size distributions and prey compositions) were consistent with the theory of resource partitioning and interspecific competition. Our first objective was to quantify species-specific relationships between three possible size metrics: fork length, gape height, and gape width to better understand morphological differences between Pacific Halibut and Arrowtooth Flounder. We then compared diets according to each metric of size to assess relative effects on trophic niche partitioning. Last, we calculated site-specific overlap in predator size (using multiple metrics) and overlap in diet compositions to assess the degree of resource partitioning between the two groundfishes.

3.3 Materials and Methods

3.3.1 Data Collection

Arrowtooth Flounder and Pacific Halibut were collected using recreational hook-and-line methods during the summer months (*i.e.,* June through August) of 2015 and 2016. The vast majority of fish were caught on guided fishing trips associated with sportfishing lodges (69.2%) or procured from private recreational anglers through dockside sampling (27.8%).

Arrowtooth Flounder were caught incidentally while fishers targeted Pacific Halibut. Heat-induced degradation of the flesh from a myxosporean parasite make for an unpalatable Arrowtooth Flounder fillet, when prepared in a manner similar to other recreationally caught fishes (Greene and Babbitt 1990). Thus, we carried out directed fishing trips to increase sample sizes for Arrowtooth Flounder as part of this study (totaling 3.0% of fish caught). All fishes were collected from nearshore waters of Southeast Alaska, within 50 km of Juneau, Alaska. For data analyses, we grouped capture locations into six generalized sites: Lynn Canal (LC), Favorite and Saginaw Channels (FS), Point Howard (PH), Funter Bay (FB), and Icy Strait (IS) (Fig. 3.1). We recorded species, capture date, site, and fork length (cm) for all retained fishes. We also measured gape height (mm) and gape width (mm) from a subsample (ATF = 26; PH = 48) of freshly dead (unfrozen) fish. We selected subsamples in order to maximize the range of fork lengths measured. Gape measurements were defined as the maximum linear distance between the upper and lower (gape height) or the right and left (gape width) sides of an extended mouth (*sensu* Scharf *et al.* 2000). Stomachs were removed and frozen until contents could be thawed, separated, and preserved using 80% ethanol. We then identified prey taxa to the lowest possible taxonomic group and separately weighed each item from non-empty stomachs. Where possible, we measured standard length (mm), body mass (kg), and carapace width (mm) for fish, cephalopod, and crab prey respectively.

3.3.2 Morphometrics

We used linear regression with an intercept fixed at zero to quantify relationships between fork length and gape height and fork length and gape width for each predator. We used analysis of covariance (ANCOVA; $\alpha = 0.1$) to test for differences in allometric growth

(*i.e.,* relationships between fork length [FL] and gape height [GH] or gape width [GW]) between Arrowtooth Flounder and Pacific Halibut. We then estimated gape heights and gape widths from individual fork lengths. We calculated overlap in size from relative fork length, gape height, and gape width frequencies for each species (Pastore 2018; Pastore and Calcagní 2019). A value of 0 indicated no overlap in size and a value of 1 represented identical size distributions.

3.3.3 Diet Compositions and Predator-Prey Size Spectra

We broadly characterized the diets of each species and size class j by calculating prey richness, Shannon diversity (H'; Shannon and Weaver 1949; Magurran 1988), and Pielou's index of evenness (J'; Pielou 1966) using lowest possible taxonomic groupings (Oksanen *et al.* 2019). Size classes were assigned to reflect ontogenetic shifts in diet compositions while maintaining adequate sample numbers. We also estimated trophic level TL for each species and size class j following Cortés (1999), such that:

$$TL_j = 1 + \left(p_{t_j} * TL_t\right) \quad (1)$$

p_{t_j} represents the proportion of prey taxa t consumed by sampling group j and TL_t is the trophic level of prey taxa t (Eqn 2). TL_t values were borrowed from Aydin *et al.* (2007). For all other analyses, we recategorized less common prey (*i.e.,* those that constituted less than 1% of prey consumed by weight) into broader taxonomic groupings (Table 3.1). We then constructed cumulative prey curves and identified sites and size classes with sufficient numbers of non-empty stomachs if curves appeared to reach an asymptote. We calculated proportions of prey by weight in the diets of predator group j (*i.e.,* unique combinations of predator species, size bin, and/or capture location) as follows:

$$p_{t_j} = \frac{\sum_{s=1}^{S} p_{t,s}}{\sum_{s=1}^{S}\sum_{t=1}^{T} p_{t,s}}, \quad (2)$$

where $p_{t,s}$ is the proportion of prey taxa t in predator stomach s. T represents the total number of prey taxa and S is the total number of predator stomachs observed (Chipps and Garvey 2007). We selected proportions of prey by weight as our dietary metric because we were interested in approximating relative energetic contributions of different prey to the diets of each predator group (Hyslop 1980). Additionally, we calculated Schoener's index of dietary overlap (Schoener 1968; Schoener 1974):

$$D_j = 1 - \frac{1}{2}\sum_{t}^{T} |p_{ATF_{t,j}} - p_{PH_{t,j}}| \quad (3)$$

p_{PH_t} and p_{ATF_t} represent proportions of prey taxa t in the diets of Arrowtooth Flounder (ATF) and Pacific Halibut (PH) and T is the total number of prey taxa observed in any given sampling group j. A value of 0 indicated no shared prey taxa and a value of 1 represented identical diet compositions. Though it is difficult to identify ecologically relevant values for what constitutes 'high' versus 'low' trophic overlap, we used D_j between 0.40 and 0.60 to represent moderate overlap (*i.e.,* overlap values that merit consideration) and D_j greater than 0.60 to signify high overlap (Zaret and Rand 1971; Ross 1986; Link and Auster 2013). We estimated dietary overlap for each comparable site and size class. We also used quantile regression to understand overlap in size-based foraging strategies between the two species (Scharf *et al.* 2000). Specifically, we regressed predator fork length, gape height, and gape width against measurements of fish, cephalopod, and crab prey size.

Finally, we used multivariate analyses to test for differences in diet composition between Arrowtooth Flounder and Pacific Halibut ('vegan' package in R; Oksanen *et al.* 2019). First, we calculated Horn-Morisita dissimilarity indices on proportional prey data with a fourth-root transformation. We selected the Horn-Morisita index over the more commonly used Bray-

Curtis dissimilarity index because it is less sensitive to differences in sample sizes among groups and it is more appropriate with mass-based proportions (Wolda 1981). Then, we used pair-wise Horn-Morisita dissimilarity values (0 = no shared prey; 1 = total shared prey in exactly the same proportions) to test for differences in beta dispersion between species, years, months, sites, and size classes (Anderson 2006; Anderson *et al.* 2006). We used a permutational multivariate analysis of variance (PERMANOVA) with Type III sums of squares (N_{perm} = 9999; α = 0.1) to test for differences in diet compositions. We selected PERMANOVA because the test relies on actual distance measures (as opposed to ranks), partitions within and among group dispersion, and has sufficient power to identify differences in centroid locations within heterogenous data (Anderson and Walsh 2013). Full models included main effects for predator species, year, month, location, and size class. We used non-metric multidimensional scaling (NMDS; Kruskal 1964) to visualize pairwise distances within each Horn-Morisita dissimilarity matrix, using the minimum number of dimensions to achieve a stress < 0.20. All statistical analyses were performed in R version 3.5.1 (R Core Team 2018). Associated script files can be found at: https://github.com/cheryl-barnes/Size_TrophicNicheSeparation.

3.4 Results

We collected 594 Arrowtooth Flounder (ATF) and 1430 Pacific Halibut (PH) during the summers of 2015 and 2016. From those subsampled for morphometrics, we found significant linear relationships between fork length and gape height ($GH_{ATF} = 2.148FL$, adjusted R^2 = 0.995, $t_{1,25}$ = 67.4, p < 0.001; $GH_{PH} = 1.115FL_{PH}$, adjusted R^2 = 0.994, $t_{1,47}$ = 86.3, p < 0.001) and between fork length and gape width ($GW_{ATF} = 2.064FL_{ATF}$, adjusted R^2 = 0.997, $t_{1,25}$ = 86.2, p < 0.001; $GW_{PH} = 1.197FL_{PH}$, adjusted R^2 = 0.993, $t_{1,47}$ = 82.6, p <

0.001) (Fig. 3.2). Gape widths also increased linearly with gape height (Fig. S3.1). We also found significant differences in allometric growth when comparing models with and without species-specific slopes (GH: $F_{1,71} = 337.7$; $p < 0.001$; GW: $F_{1,71} = 353.5$; $p < 0.001$). Although the median fork length for Arrowtooth Flounder (56 cm) was 29.1% smaller than that of Pacific Halibut (79 cm), the median predicted gape height was 34.8% larger (ATF: 120 mm; PH: 89 mm) and the median gape width was 21.1% larger (ATF: 115 mm; PH: 95 mm). We found minimal overlap in fork length frequencies across sampling sites (0.084 ± 0.048; Fig. 3.3). Relative frequencies for predicted gape height reflected a greater degree of overlap between the two groundfish predators (0.146 ± 0.026) and predicted gape widths displayed the greatest overlap in size across sites (0.254 ± 0.044).

A total of 169 (28.5%) Arrowtooth Flounder and 920 (64.3%) Pacific Halibut stomachs contained prey. Predator fork lengths for these fish measured 44 to 94 cm for Arrowtooth Flounder (GH: 94 to 202 mm; GW: 90 to 194 mm) and 32 to 158 cm (GH: 35 to 177 mm; GW: 38 to 190 mm) for Pacific Halibut. Overall, Pacific Halibut diets were more speciose, exhibited greater trophic diversity, and had proportions of prey that were more evenly distributed across taxa (Table 3.2). Trophic levels were similar between the two predators, with Arrowtooth Flounder feeding at a slightly higher level than Pacific Halibut with the same size fork length and gape height bins (Table 3.3). Arrowtooth Flounder diets consisted primarily of Pacific Herring (*Clupea pallasii*; 0.308), squids (order Teuthida; 0.213), and Walleye Pollock (*Gadus chalcogrammus*; 0.210), with larger individuals consuming more fishes and less squids (Fig. 3.4). Gadids (*i.e.,* Walleye Pollock and Pacific Cod [*Gadus macrocephalus*]) comprised the greatest proportion (0.361) of Pacific Halibut diets, followed by Pacific Herring (0.195), and a wide variety of crustaceans, cephalopods, and other fishes (Fig. 3.4). Larger Pacific Halibut tended to consume more pollock, more octopuses, and

less herring than smaller conspecifics. Halibut with the largest gape heights, however, consumed less pollock than those in preceding size classes.

We had sufficient sample sizes to compare diets of Arrowtooth Flounder and Pacific Halibut within the 60 and 69 cm fork length bin and 96 to 155 mm gape height and gape width bins (Fig. S3.2). We also compared species- and size-specific diets according to generalized capture sites to gain a better understanding about how resource use varied at relatively fine spatial scales. Lynn Canal, Favorite-Saginaw Channels, and Point Howard yielded adequate numbers of both species were caught. We found moderate to high dietary overlap between the two groundfish predators. Dietary overlap varied by location and size class. Spatially, overlap in diet was highest at Point Howard, followed by Favorite-Saginaw Channels and Lynn Canal (Fig. 3.5). Fish measuring between 60 and 69 cm fork length showed high overlap in diets (Fig. 3.6). Gape widths between 96 and 115 mm (~ ATF_{FL}: 46 to 55 cm and PH_{FL}: 80 to 96 cm) exhibited the greatest degree of dietary overlap by size and gape widths between 116 and 135 mm (~ ATF_{FL}: 56 to 65 cm and PH_{FL}: 97 to 113 cm) showed the lowest overlap in diet. Gape heights from 96 to 115 mm (~ ATF_{FL}: 44 to 53 cm and PH_{FL}: 86 to 103 cm) also displayed higher overlap in diet compared to those measuring between 116 and 135 mm (~ ATF_{FL}: 54 to 53 cm and PH_{FL}: 104 to 121 cm).

Despite overlapping diet compositions, we found noticeable differences in predator size-prey size relationships. Both the maximum and the range of prey sizes (fishes and crabs) consumed by Pacific Halibut increased with increasing predator size (Fig. 3.7; Table 3.4). Estimates of cephalopod body mass consumed by Pacific Halibut were highly variable. The range of predator sizes and numbers of measurable fish and cephalopod prey were much smaller for Arrowtooth Flounder. Arrowtooth Flounder stomachs did not contain any measurable crabs.

We found significant multivariate differences in diet compositions between Pacific Halibut and Arrowtooth Flounder in three of the four size categories tested ($p < 0.1$; Fig. 3.8). The 96 to 135 mm gape width bin was the only size class that showed no difference in diet compositions between Arrowtooth Flounder and Pacific Halibut. The 96 to 115 mm gape width bin was also the only size class with a significant difference in dispersion between the two species, with greater dietary dispersion for Arrowtooth Flounder ($F_{1,25} = 4.397$, $p = 0.063$). In addition to differences in diet compositions between predators, we found an effect of month when grouping diet data by fork length ($F_{2,19} = 1.749$, $r^2 = 0.142$, $p = 0.082$) and an effect of size when grouping diet data by gape width ($F_{1,56} = 2.732$, $r^2 = 0.042$ $p = 0.030$) (Fig. S3.3).

3.5 Discussion

We found significant differences in allometric growth between Arrowtooth Flounder and Pacific Halibut. Disparate relationships between fork length and gape height or gape width were reflected in estimates of size overlap, with small-bodied but large-gaped Arrowtooth Flounder and relatively large-bodied but small-gaped Pacific Halibut sampled at any given location. Although only three sites yielded sufficient sample sizes to compare diets of these predators, we found increases in dietary overlap with increasing overlap in size. Dietary overlap was generally moderate to high in Southeast Alaska. Fishes with smaller gape sizes displayed greater diet similarity than those with larger gapes, which appeared to more effectively partition prey (*i.e.,* Arrowtooth Flounder consumed more Pacific Herring and Pacific Halibut consumed more gadids and invertebrates). Despite substantial dietary overlap and similar trophic level estimates, we found significant differences in prey compositions by species and gape width. Pacific Halibut diets were more diverse and

evenly distributed than those of Arrowtooth Flounder. The size range of prey consumed by Pacific Halibut was also greater and increased with increasing predator size. Due to small sample sizes of measurable prey, relationships between predator size and prey size should be considered preliminary for Arrowtooth Flounder.

3.5.1 Morphometric Effects on Trophic Niche Separation

Greater similarity of prey consumed by Arrowtooth Flounder and Pacific Halibut with smaller gapes provides support for the hypothesis that size is more important than phylogeny in determining the functional role of organisms (Jennings *et al.* 2002). We emphasize that the metric of size used to compare diets among potentially competing species also warrants consideration, especially given differences in dietary overlap between small and large gape width bins. When different allometric growth is measured, a variety of potential morphological constraints (*e.g.,* Wainwright 1988; Krebs and Turingan 2003; Mihalitsis and Bellwood 2017) should be assessed prior to evaluating resource partitioning.

Of the size metrics examined, we conclude that gape width was the most appropriate measurement for comparing diets of Arrowtooth Flounder and Pacific Halibut. We found evidence for trophic partitioning among fishes with relatively large gapes. As gape sizes increased, Arrowtooth Flounder consumed more herring and Pacific Halibut consumed greater proportions of pollock/cod. These differences in prey composition could have been affected by different habitat associations or prey capture abilities associated with disparate fork lengths within a given size class for gape. Differences in diets could also have resulted from fine-scale differences in habitat use according to depth or temperature gradients (Yamada pers. obs.). The addition of quality environmental data would help explain variation in diets due to abiotic factors. Regardless, relatively high dietary overlap among

fishes with smaller gapes suggests increased potential for competition at earlier life stages (*e.g.,* Piet *et al.* 1998). Evidence of gape limitation from predator-prey size spectra (*i.e.,* the decreased range of prey sizes consumed at smaller predator gape sizes) corroborate this conclusion (Schmitt and Holbrook 1999). A diet study focused on smaller Arrowtooth Flounder would aid in the comparative assessment of gape limitation for both species.

The primary focus of this study was to understand size-specific differences in the diets of our focal species. We also qualitatively assessed site-based variation in prey compositions to understand fine-scale differences in foraging patterns of Pacific Halibut and Arrowtooth Flounder. Within morphological constraints, flatfishes tend to feed opportunistically according to localized prey abundance (Link *et al.* 2005). Thus, we expected that predator-specific diet compositions would shift similarly from one site to the next, in response to local prey densities. Among our three sites, we observed differences in diet compositions for Arrowtooth Flounder. We also observed differences in dietary overlap between the two predators, which generally increased from north to south. Interestingly, greater dietary overlap coincided with greater overlap in gape size, but not body size. This supports our supposition that differences in size (using the most appropriate size metric) must be accounted for in order to separate out effects of time and place. In locations and time periods with high overlap in size, differences in diets should reflect actual trophic niche separation by way of resource partitioning.

One potential issue with observing fine-scale spatial differences in diets is that heterogeneity may mask our ability to detect resource partitioning at broader spatial scales. We inferred trophic niche separation at local levels in nearshore Southeast Alaska (2015 to 2016). Barnes *et al.* (2018) used long-term survey data (1990 to 2013) to quantify the relationship between spatial overlap and dietary overlap, and found no evidence of niche

complementarity throughout the Gulf of Alaska. However, dietary overlap was generally low throughout the region. As such, we are confronted with the issue of scale and how best to move from individual observations to population-level effects (Levin 1992). Because different resources are limiting at different spatial and temporal scales (*e.g.,* Munday *et al.* 2001), a (sub)regional assessment of spatial and dietary overlap using gape widths as the metric of size would be fruitful. This type of research would elucidate whether or not dietary overlap is higher than previously thought, when based on gape widths rather than fork lengths.

3.5.2 Inferences about Competitive Superiority

Typically, large-bodied fishes are considered superior competitors because enhanced swimming abilities (Beamish 1978) and better visual acuity (Walton *et al.* 1994) allow them to better occupy suitable habitats and capture optimal prey (Schoener 1982; Ross 1986; Ward *et al.* 2006). Larger predators also have the competitive advantage of being able to feed on a wide range of prey (Scharf et al. 2000). Inferior competitors, on the other hand, are able to gain access to preferred resources only through increased relative body size or prior residency (*i.e.,* the home field advantage) (Munday *et al.* 2001). Although we did not assess potential differences in prey capture as a function of body size, the relatively large body size, prominent eyes, strong jaws and musculature, and general hardiness of Pacific Halibut (Barnes pers. obs.) likely make it a superior competitor to Arrowtooth Flounder. Differences in allometric growth may, however, stimulate exploitative competition between adult Arrowtooth Flounder and halibut at earlier life stages (Connell 1983, Schoener 1983).

The exceptionally large gape sizes of Arrowtooth Flounder enable an early onset of piscivory (Mittelbach and Persson 1998), thereby promoting faster growth and development

(Keast 1985; Juanes 1994; Mittelbach and Persson 1998) – a physiological win for Arrowtooth Flounder. For instance, Arrowtooth Flounder consume substantial amounts of Pacific Herring, which have high lipid content relative to other commonly ingested prey (Anthony *et al.* 2000). Pacific Halibut have much smaller gapes at similar fork lengths, increasing the likelihood that they experience decreased access to nutrient-rich prey as juveniles. Instead, their strong jaws are better adapted to consuming hard-bodied invertebrates (*e.g.,* Keast and Webb 1966) not consumed by Arrowtooth Flounder. Strong swimming capabilities also enable the capture of more evasive prey such as octopuses, which may present too extensive of handling times for Arrowtooth Flounder (*e.g.,* Nilsson and Brönmark 2000).

The more diverse diets of Pacific Halibut, which encompass nearly all prey types consumed by Arrowtooth Flounder, could represent greater adaptability during periods of decreased resource availability. Increased trophic niche breadth could also represent dietary switching as a means of alleviating negative effects from competition (Colwell and Fuentes 1975). Similar patterns of more generalist and more specialist diets have been observed for native and non-native fishes, respectively (Juncos *et al.* 2014). Regardless of trophic niche breadth or physiological adaptations, continued coexistence may be possible because each species is the competitive superior at different times or in different components of their shared niche space (Colwell and Fuentes 1975).

3.6 Acknowledgments

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3.8 Figures

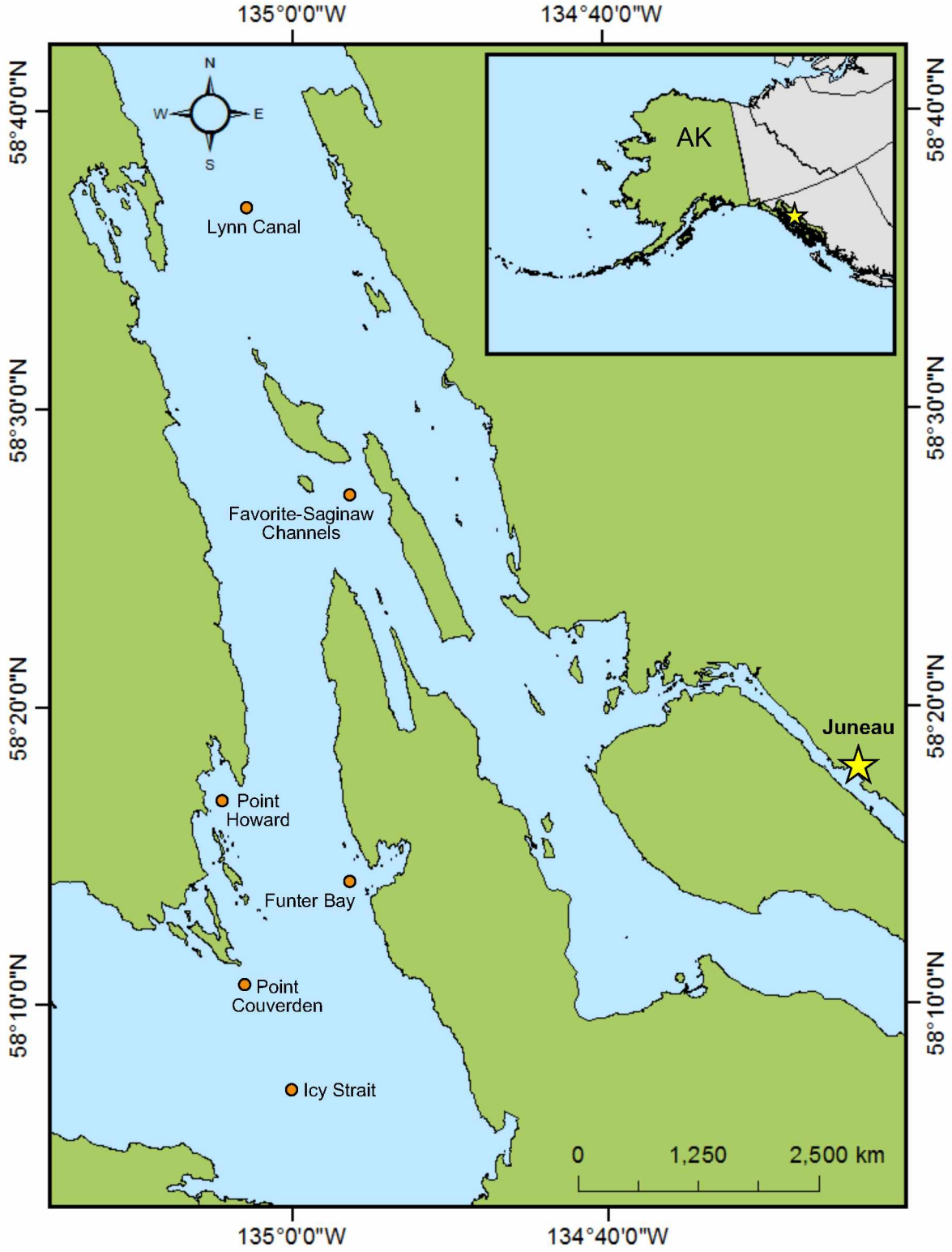


Figure 3.1 Primary sites used to sample Arrowtooth Flounder and Pacific Halibut for gut content analysis (Southeast Alaska, 2015 to 2016).

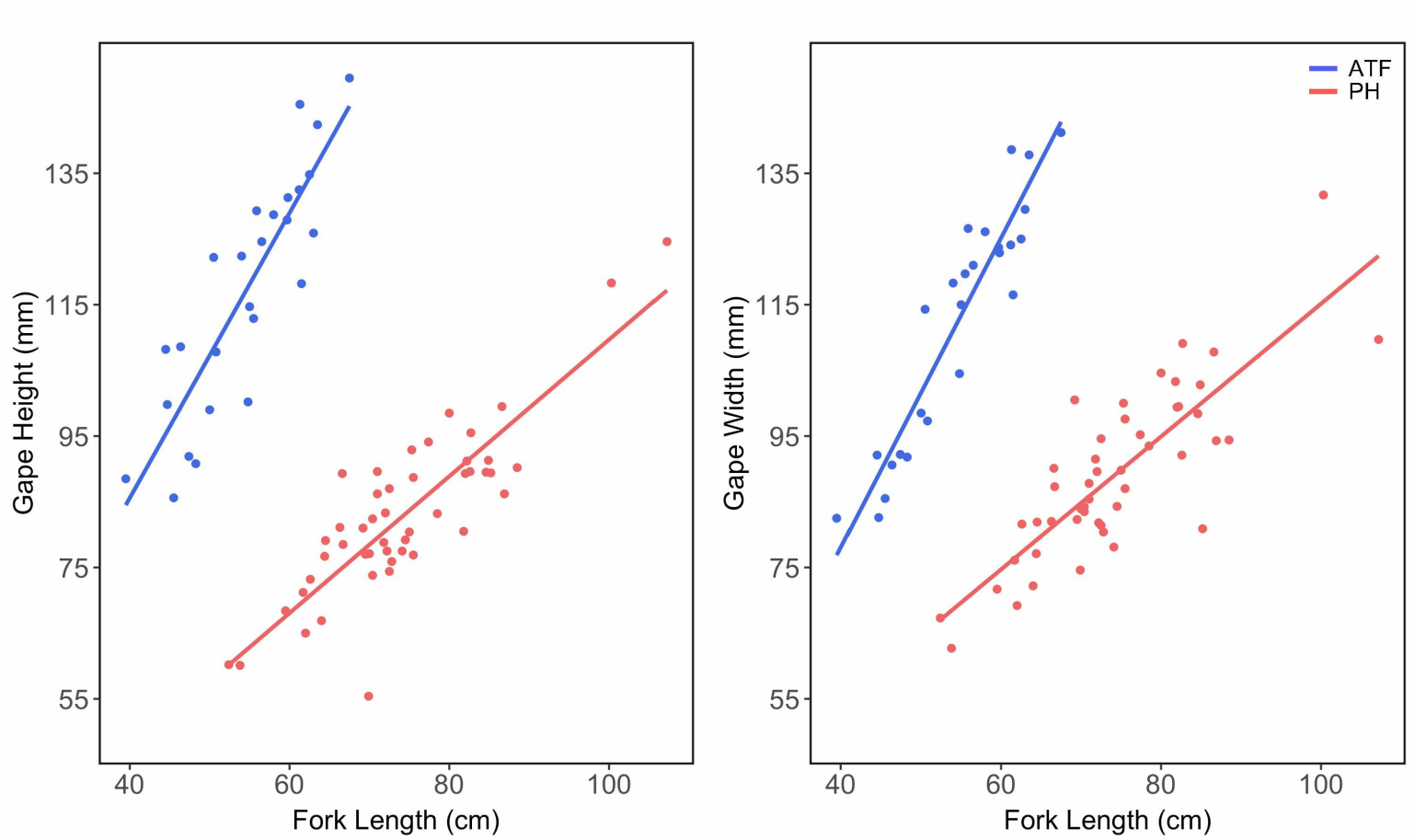


Figure 3.2 Relationships between fork length and gape height (left) and fork length and gape width (right) for Arrowtooth Flounder (ATF; blue) and Pacific Halibut (PH; red), Southeast Alaska (2015 to 2016).

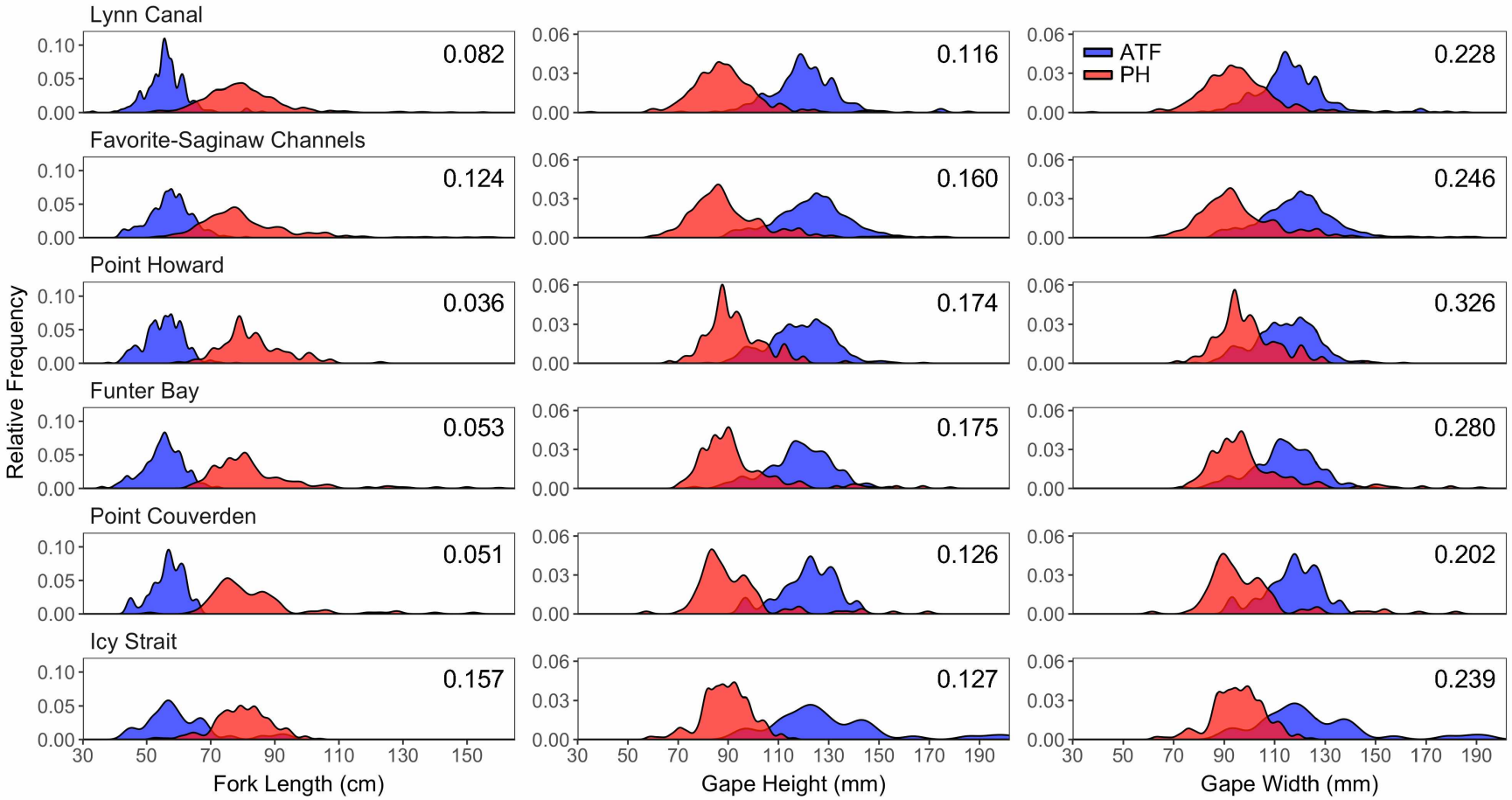


Figure 3.3 Relative frequency distributions for Arrowtooth Flounder (ATF; blue) and Pacific Halibut (PH; red) by sampling site and size measurement (Southeast Alaska, 2015 and 2016). Overlap estimates are shown (upper-right corner) for each combination of site and metric of size (left: fork length [mm], center: gape height [mm], right: gape width [mm]).

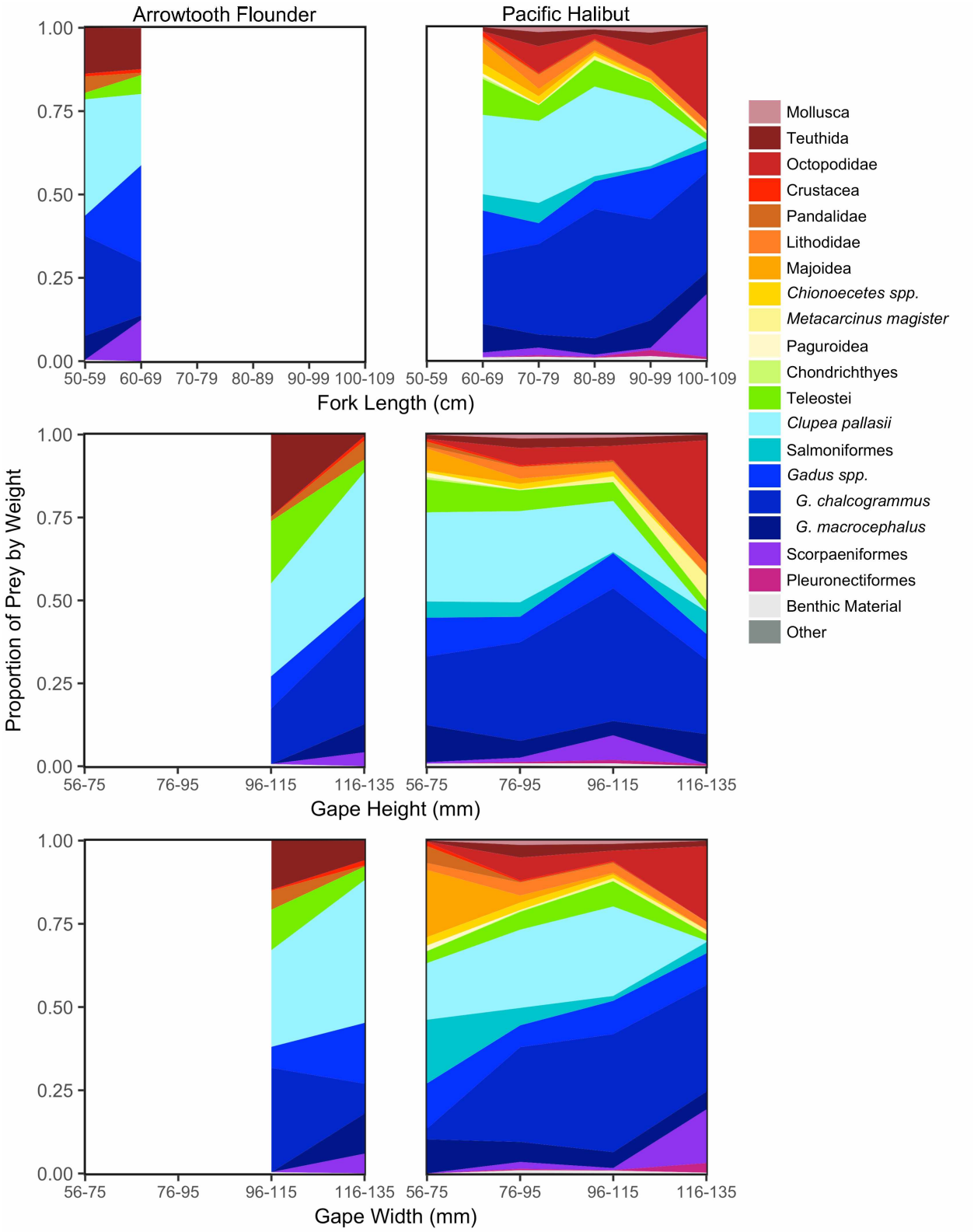


Figure 3.4 Proportions of prey by weight for Arrowtooth Flounder and Pacific Halibut by size class (Southeast Alaska, 2015 and 2016). Only fork length (top), gape height (middle), and gape width (bottom) bins with sufficient sample sizes (n ≥ 20) are shown.

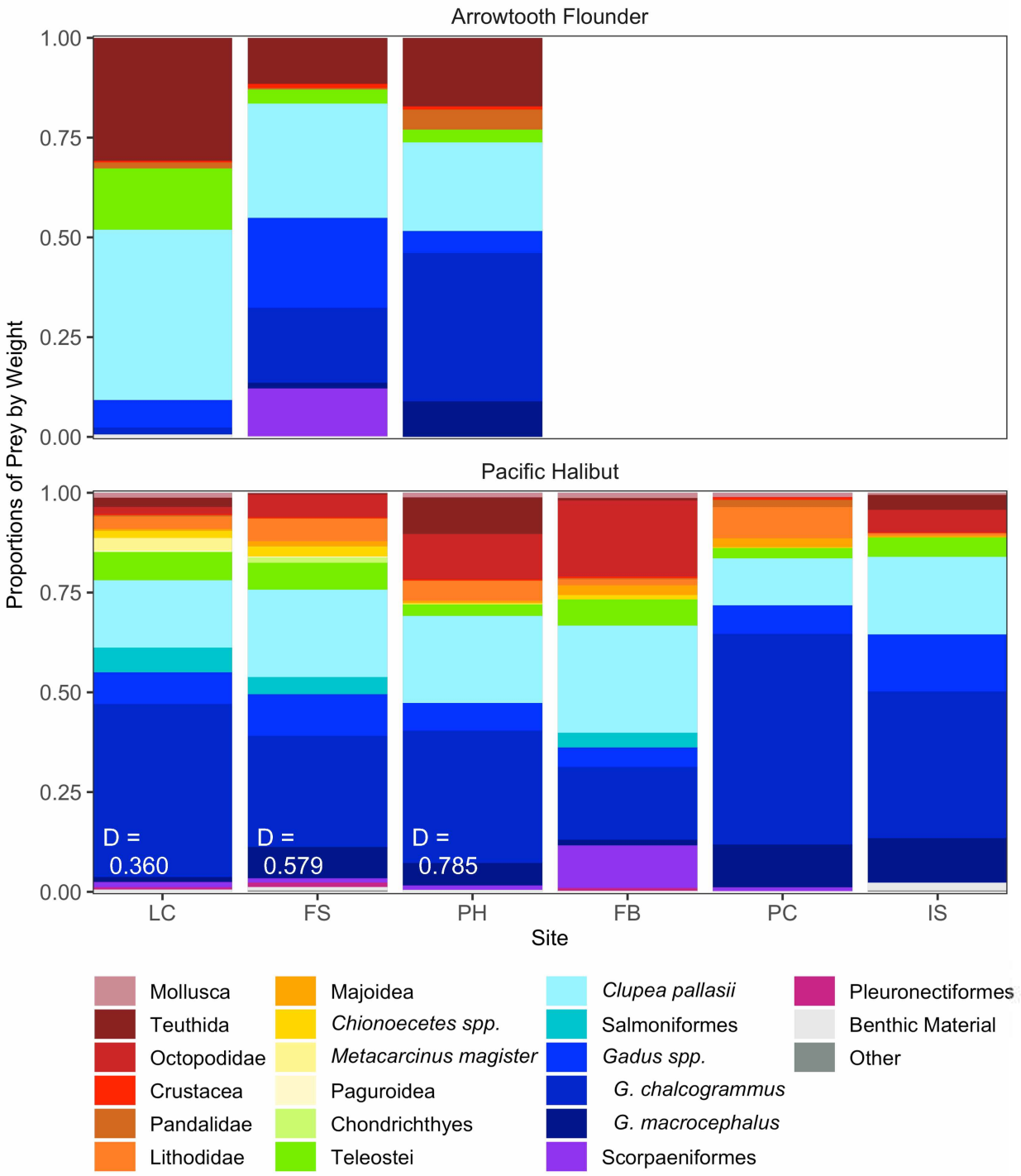


Figure 3.5 Proportions of prey by weight for Arrowtooth Flounder and Pacific Halibut with 96 to 115 mm gape widths (Southeast Alaska, 2015 and 2016). Sampling sites are shown from north to south, left to right. LC: Lynn Canal, FS: Favorite-Saginaw Channels, PH: Point Howard, FB: Funter Bay, PC: Point Couverden, and IS: Icy Strait. Schoener's index of dietary overlap (D; Schoener 1974; Schoener 1983) is shown for each site with sufficient samples (all sizes combined).

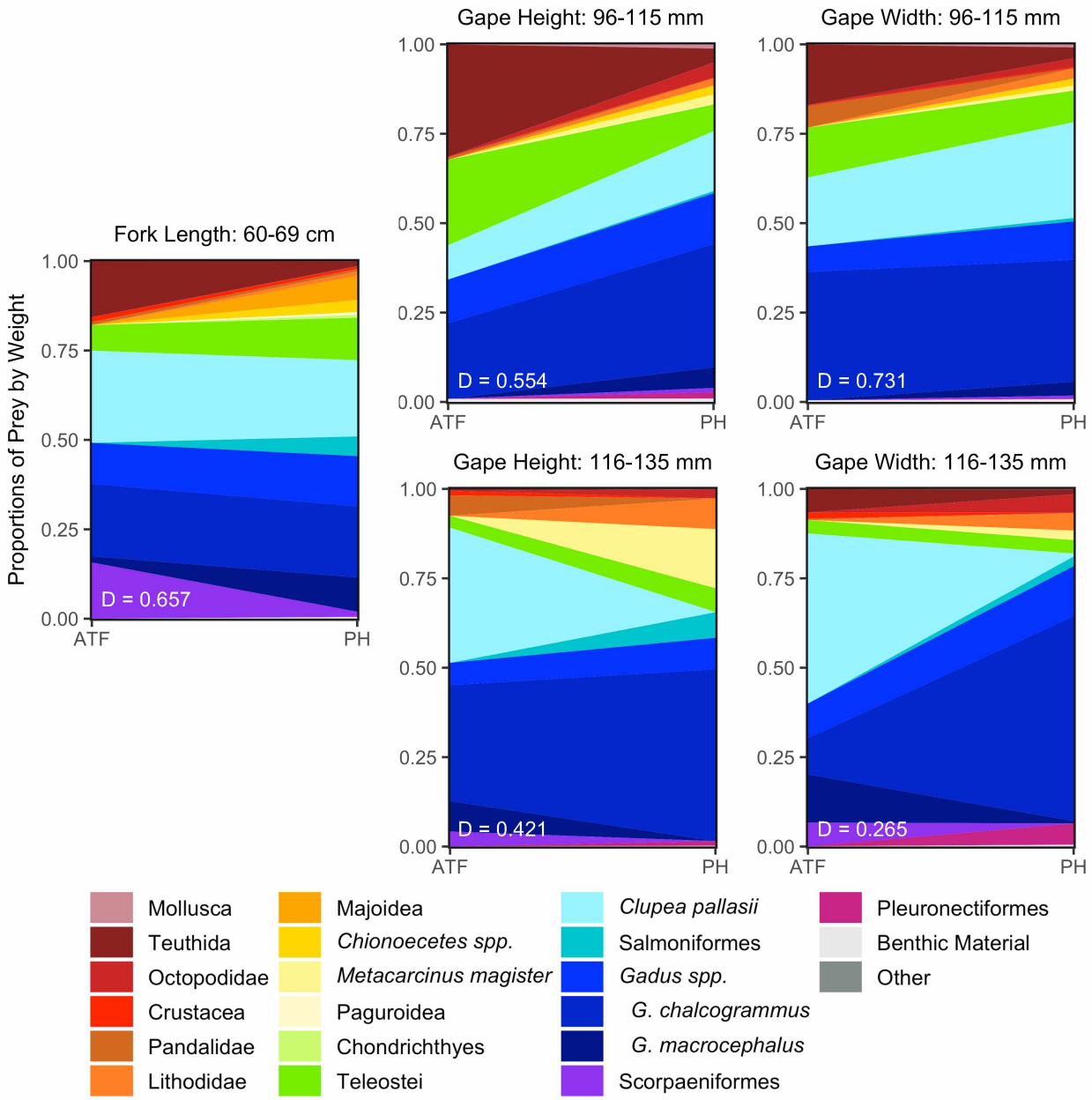


Figure 3.6 Proportions of prey by weight for overlapping size bins of Arrowtooth Flounder (ATF) and Pacific Halibut (PH) from Lynn Canal, Favorite-Saginaw Channels, and Point Howard (Southeast Alaska, 2015 and 2016). Schoener's index of dietary overlap (D; Schoener 1974; Schoener 1983) is shown for each size bin. Left: ATF and PH measuring 60-69 cm fork length; Center: ATF and PH measuring 96-115 (top) and 116-135 (bottom) mm gape height; Right: ATF and PH measuring 96-115 (top) and 116-135 (bottom) mm gape width.

a)

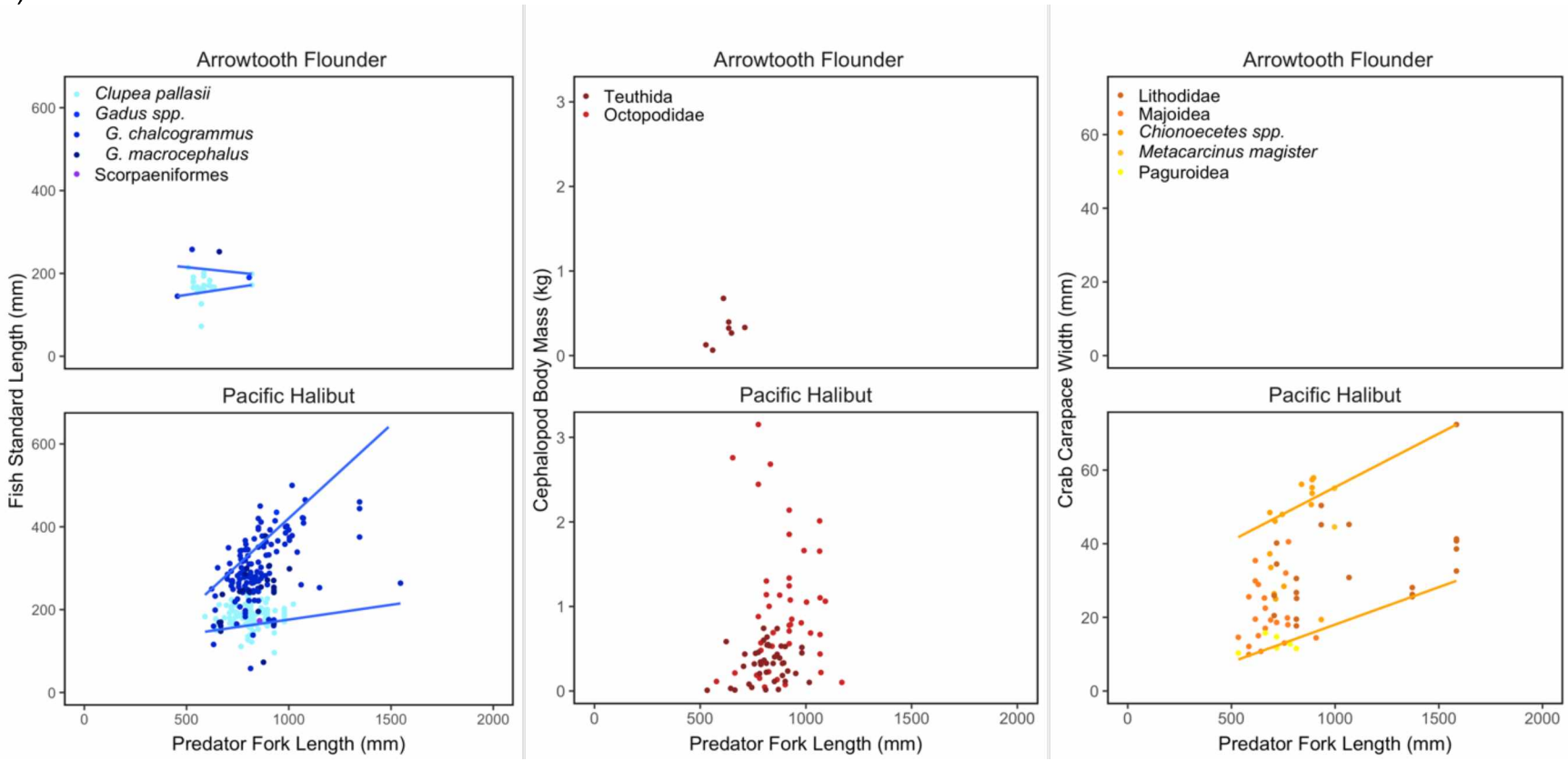


Figure 3.7 Relationships between predator size and prey size from Arrowtooth Flounder (top) and Pacific Halibut (bottom) sampled in Lynn Canal, Favorite-Saginaw Channels, and Point Howard (Southeast Alaska, 2015 to 2016). Size spectra are shown by predator a) fork length, b) gape height, and c) gape width. Lines represent 10th and 90th quantiles. Standard lengths (mm) for fish prey are shown in blue (left), cephalopod body masses (kg) are shown in red (center), and carapace widths for crabs (mm) are shown in orange (right).

b)

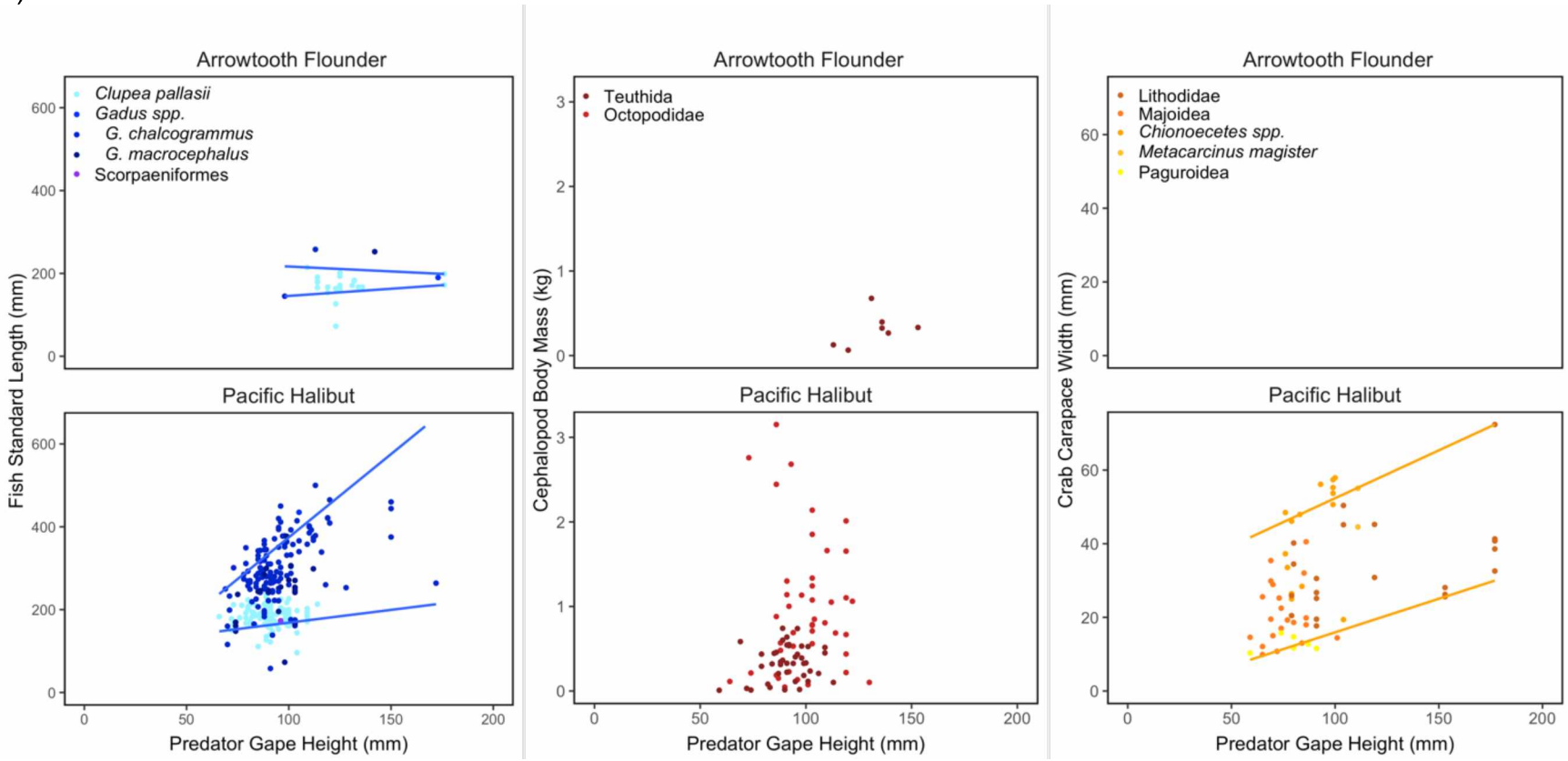


Figure 3.7 (cont) Relationships between predator size and prey size from Arrowtooth Flounder (top) and Pacific Halibut (bottom) sampled in Lynn Canal, Favorite-Saginaw Channels, and Point Howard (Southeast Alaska, 2015 to 2016). Size spectra are shown by predator a) fork length, b) gape height, and c) gape width. Lines represent 10th and 90th quantiles. Standard lengths (mm) for fish prey are shown in blue (left), cephalopod body masses (kg) are shown in red (center), and carapace widths for crabs (mm) are shown in orange (right).

c)

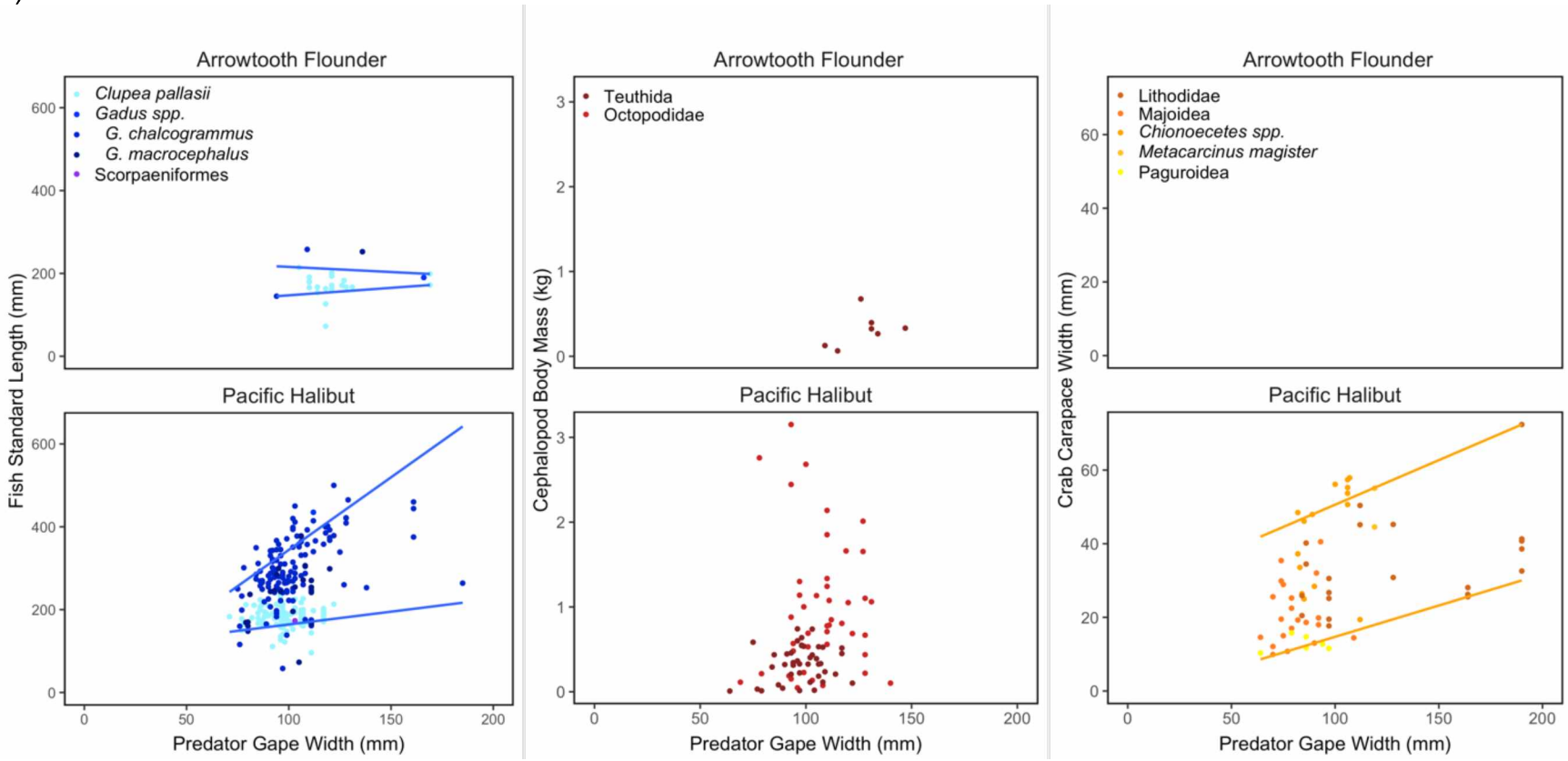


Figure 3.7 (cont) Relationships between predator size and prey size from Arrowtooth Flounder (top) and Pacific Halibut (bottom) sampled in Lynn Canal, Favorite-Saginaw Channels, and Point Howard (Southeast Alaska, 2015 to 2016). Size spectra are shown by predator a) fork length, b) gape height, and c) gape width. Lines represent 10th and 90th quantiles. Standard lengths (mm) for fish prey are shown in blue (left), cephalopod body masses (kg) are shown in red (center), and carapace widths for crabs (mm) are shown in orange (right).

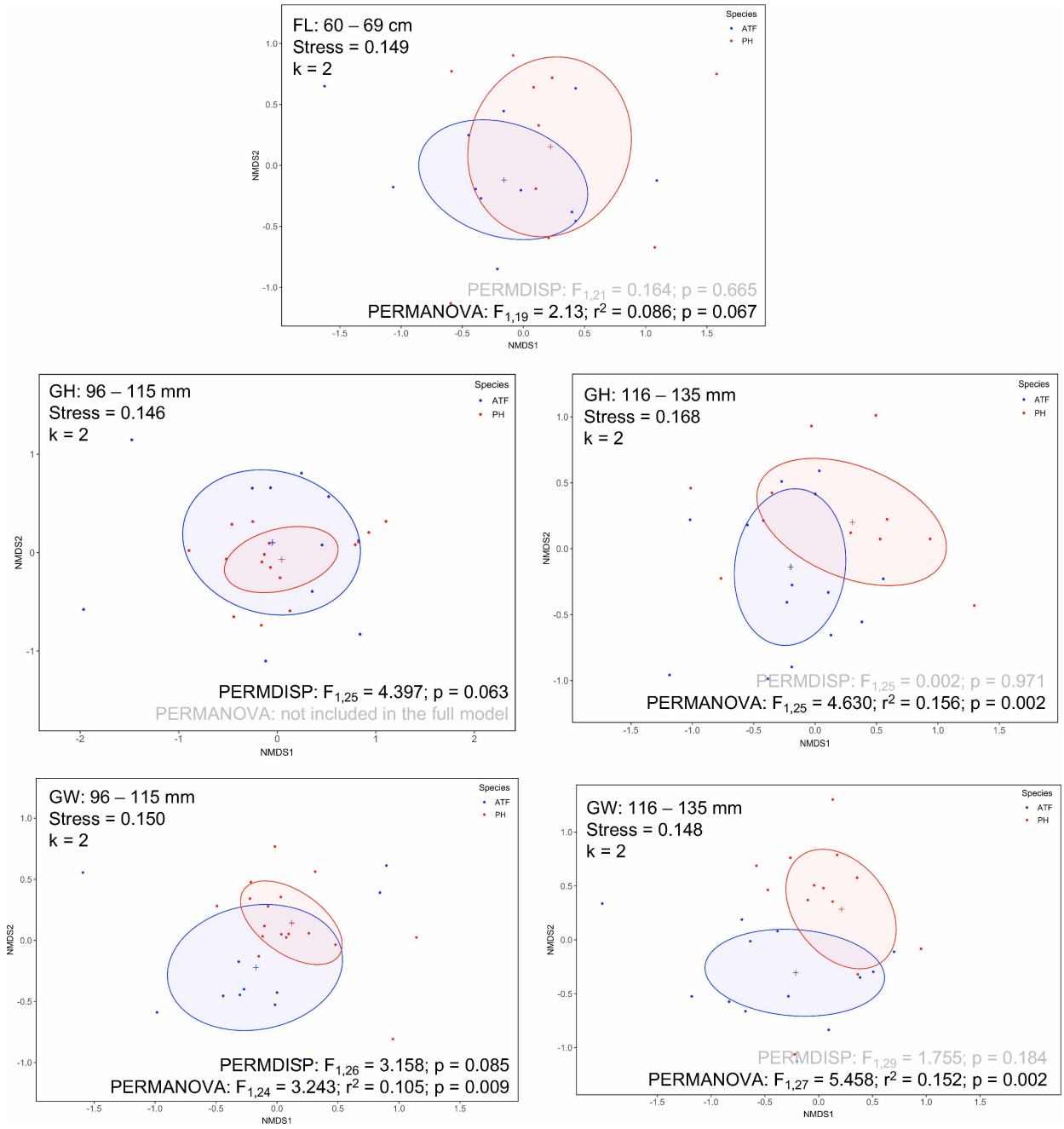


Figure 3.8 Non-metric multidimensional scaling plots depicting diet compositions for Arrowtooth Flounder (ATF; blue) and Pacific Halibut (PH; red) in Southeast Alaska (Lynn Canal, Favorite-Saginaw Channels, and Point Howard sites only; 2015 to 2016). Each comparable size bin for fork length (FL, top), gape height (GH, middle), and gape width (GW, bottom) are shown. Ellipses represent 95% confidence intervals. Stress estimates and number of dimensions (k) are listed for each size bin.

3.9 Tables

Table 3.1 Proportions by weight for each prey taxa observed in stomach contents of Arrowtooth Flounder (ATF) and Pacific Halibut (PH), Southeast Alaska (all sizes and sites; 2015 to 2016). Lowest possible (*i.e.,* original) taxonomic assignments and taxonomic regroupings are listed. Bolded values highlight prey taxa that comprised ≥ 0.01 of diets.

Taxonomic Regrouping	Original Taxonomic Assignment	ATF	PH
Mollusca	Bivalvia		< 0.001
	Cephalopoda	0.001	0.007
	Gastropoda		< 0.001
	Mollusca		0.001
	Mytilidae		< 0.001
	Rossia pacifica		0.001
Teuthida	***Berryteuthis magister***	**0.173**	0.005
	Teuthida	**0.020**	**0.020**
Octopodidae	***Enteroctopus dofleini***		**0.056**
	Octopodidae		**0.018**
Crustacea	Amphipoda		
	Argis dentata	< 0.001	
	Caridea		< 0.001
	Crangon sp.	< 0.001	
	Heptacarpus brevirostris		< 0.001
	Isopoda	0.001	< 0.001
	Pasiphaea pacifica	0.004	< 0.001
	Pasiphaeidae		< 0.001
	Pleocyemata	0.002	0.003
Pandalidae	Pandalidae	0.003	< 0.001
	Pandalopsis dispar	0.004	< 0.001
	Pandalus sp.	0.001	< 0.001
	Pandalus borealis	0.001	
	Pandalus goniurus	0.002	< 0.001
	Pandalus platyceros	0.004	0.002
Lithodidae	*Acantholithodes hispidus*		0.006
	Lithodes aequispinus		**0.014**
	Lithodidae		**0.010**
	Lopholithodes foraminatus		0.006
	Paralithodes camtschaticus		0.001
	Rhinolithodes wosnessenskii		0.001
Majoidea	*Chorilia longipes*		0.001
	Hyas lyratus		**0.011**
Chionoecetes spp.	*Chionoecetes sp.*		0.001
	Chionoecetes bairdi		**0.012**
Metacarcinus magister	*Metacarcinus magister*		0.009
Paguroidea	Diogenidae		< 0.001
	Elassochirus cavimanus		< 0.001
	Paguridae		0.001
	Paguroidea		0.001

Table 3.1 (cont) Proportions by weight for each prey taxa observed in stomach contents of Arrowtooth Flounder (ATF) and Pacific Halibut (PH), Southeast Alaska (all sizes and sites; 2015 to 2016). Lowest possible (*i.e.,* original) taxonomic assignments and taxonomic regroupings are listed. Bolded values highlight prey taxa that comprised ≥ 0.01 of diets.

Taxonomic Regrouping	Original Taxonomic Assignment	ATF	PH
Chondrichthyes	Chondrichthyes		0.001
	Rajidae		0.002
Teleostei	*Lycodes spp.*		0.002
	Stichaeus punctatus	0.006	
	Teleostei	**0.066**	**0.056**
Clupea pallasii	***Clupea pallasii***	**0.336**	**0.203**
Salmoniformes	*Oncorhynchus gorbuscha*		0.005
	Oncorhynchus keta		0.003
	Salmonidae		**0.026**
Gadus sp.	***Gadus sp.***	**0.115**	**0.083**
Gadus chalcogrammus	***Gadus chalcogrammus***	**0.188**	**0.361**
Gadus macrocephalus	***Gadus macrocephalus***	**0.039**	**0.049**
Scorpaeniformes	Cottidae		0.005
	Odontopyxis trispinosa		< 0.001
	Scorpaeniformes		< 0.001
	Sebastidae	**0.018**	**0.023**
Pleuronectiformes	*Atheresthes stomias*		0.003
	Bothidae		0.001
	Pleuronectiformes		0.002
Benthic Material	Cnidaria		< 0.001
	Derbesia marina		< 0.001
	Echinoidea		0.001
	Melonchela clathriata		< 0.001
	Mycale loveni		< 0.001
	Ochrophyta	< 0.001	< 0.001
	Ophiuroidea	< 0.001	< 0.001
	Phyllospadix		< 0.001
	Plantae		< 0.001
	Polychaeta		< 0.001
	Porifera	0.002	0.001
	Rhodophyta		< 0.001
	Rock and/or Shell Hash	< 0.001	0.003
	Soranthera ulvoidea		< 0.001
Other	Craniata		< 0.001
	Gallus gallus		0.001
	Homo sapiens		< 0.001
	Unidentified Inorganic Material		< 0.001
	Unidentified Organic Matter		< 0.001

Table 3.2 Diet metrics for Arrowtooth Flounder (ATF) and Pacific Halibut (PH) by a) fork length, b) gape height, and c) gape width (Lynn Canal, Favorite-Saginaw Channels, and Point Howard sites only; 2015 to 2016). S: prey richness; H': Shannon index of diversity; J': Pielou's index for evenness; n: sample size (≥ 20).

a) Fork Length (cm)

	50-59	60-69	70-79	80-89	90-99	100-109	All size classes
ATF							
S	16	12	-	-	-	-	19
H'	1.69	1.87	-	-	-	-	1.87
J'	0.55	0.55	-	-	-	-	0.51
n	80	52	-	-	-	-	132
PH							
S	-	26	46	34	23	14	59
H'	-	2.32	2.36	1.78	2.27	1.33	2.26
J'	-	0.68	0.61	0.50	0.71	0.49	0.55
n	-	59	206	180	68	39	552

b) Gape Height (mm)

	56-75	76-95	96-115	116-135	136-155	156-175	All size classes
ATF							
S	-	-	13	16	-	-	21
H'	-	-	1.69	1.67	-	-	1.98
J'	-	-	0.46	0.50	-	-	0.51
n	-	-	41	95	-	-	136
PH					-	-	
S	28	52	33	17	-	-	59
H'	2.26	2.19	2.17	1.63	-	-	2.28
J'	0.67	0.55	0.59	0.49	-	-	0.54
n	56	348	143	25	-	-	572

c) Gape Width (mm)

	56-75	76-95	96-115	116-135	136-155	156-175	All size classes
ATF							
S	-	-	15	13	-	-	21
H'	-	-	1.76	1.67	-	-	1.98
J'	-	-	0.47	0.51	-	-	0.51
n	-	-	66	75	-	-	141
PH					-	-	
S	17	51	38	20	-	-	59
H'	2.09	2.36	2.00	1.63	-	-	2.28
J'	0.72	0.60	0.53	0.50	-	-	0.54
n	21	260	233	54	-	-	568

Table 3.3 Trophic level estimates for Arrowtooth Flounder (ATF) and Pacific Halibut (PH) by fork length (FL, cm), gape height (GH, mm), and gape width (GW, mm) (2015 to 2016). Lynn Canal, Favorite-Saginaw Channels, and Point Howard sampling sites only (n ≥ 20).

a) Fork Length (cm)

	50-59	60-69	70-79	80-89	90-99	100-109	All size classes
ATF	4.54	4.61	-	-	-	-	4.55
PH	-	4.56	4.59	4.57	4.58	4.56	4.58

b) Gape Height (mm)

	56-75	76-95	96-115	116-135	136-155	156-175	All size classes
ATF	-	-	4.62	4.53	-	-	4.56
PH	4.53	4.58	4.57	4.50	-	-	4.57

c) Gape Width (mm)

	56-75	76-95	96-115	116-135	136-155	156-175	All size classes
ATF	-	-	4.56	4.57	-	-	4.56
PH	4.45	4.59	4.56	4.59	-	-	4.57

Table 3.4 Quantile regression results for Pacific Halibut and Arrowtooth Flounder predator-prey size spectra, by predator size metric and prey group (Southeast Alaska, 2015 to 2016). Prey group measurements: standard lengths (mm) for fishes, body masses (kg) for cephalopods, and carapace widths for crabs (mm). Standards errors shown in parentheses. Models with non-significant slopes are grayed out. No carapace widths were measured from Arrowtooth Flounder prey.

a) Arrowtooth Flounder

Size Metric	Prey Group	τ	α	t_α	p_α	β	t_β	p_β
FL (mm)	fishes	0.1	544 (53)	10.3	< 0.001	- 0.1 (0.3)	- 0.2	0.829
		0.9	430 (126)	3.4	0.002	2.0 (0.9)	2.1	0.045
GH (mm)	fishes	0.1	116 (12)	9.6	< 0.001	- 0.0 (0.1)	- 0.2	< 0.001
		0.9	93 (28)	3.3	0.003	0.4 (0.2)	2.1	0.051
GW (mm)	fishes	0.1	112 (11)	10.0	< 0.001	- 0.0 (0.1)	- 0.2	0.865
		0.9	89 (26)	3.5	0.002	0.4 (0.2)	2.2	0.042
FL (mm)	cephalopods	0.1	508 (50)	10.1	< 0.001	151.0 (121.7)	1.2	0.270
		0.9	523 (116)	4.5	0.006	567.1 (523.8)	1.1	0.328
GH (mm)	cephalopods	0.1	109 (11)	10.1	< 0.001	32.7 (25.8)	1.3	0.261
		0.9	112 (26)	4.4	0.007	123.1 (115.7)	1.1	0.336
GW (mm)	cephalopods	0.1	105 (10)	10.1	< 0.001	30.9 (25.3)	1.2	0.277
		0.9	107 (24)	4.4	0.007	119 (110)	1.1	0.328

Table 3.4 (cont) Quantile regression results for a) Arrowtooth Flounder and b) Pacific Halibut predator-prey size spectra, by predator size metric and prey group (Southeast Alaska, 2015 to 2016). Prey group measurements: standard lengths (mm) for fishes, body masses (kg) for cephalopods, and carapace widths for crabs (mm). Standards errors shown in parentheses. Models with non-significant slopes are grayed out. No carapace widths were measured from Arrowtooth Flounder prey.

b) Pacific Halibut

Size Metric	Prey Group	τ	α	t_α	p_α	β	t_β	p_β
FL (mm)	fishes	0.1	564 (36)	15.7	< 0.001	0.6 (0.1)	4.7	< 0.001
		0.9	815 (26)	31.4	< 0.001	0.6 (0.1)	5.4	< 0.001
GH (mm)	fishes	0.1	62 (4)	15.4	< 0.001	0.1 (0.0)	4.9	< 0.001
		0.9	91 (3)	31.3	< 0.001	0.1 (0.0)	5.4	< 0.001
GW (mm)	fishes	0.1	68 (4)	15.9	< 0.001	0.1 (0.0)	4.5	< 0.001
		0.9	98 (3)	30.9	< 0.001	0.1 (0.0)	5.2	< 0.001
FL (mm)	cephalopods	0.1	698 (24)	28.7	< 0.001	24.5 (22.3)	1.1	0.275
		0.9	991 (44)	22.3	< 0.001	44.4 (55.2)	0.8	0.423
GH (mm)	cephalopods	0.1	78 (3)	29.2	< 0.001	2.4 (2.5)	1.0	0.333
		0.9	110 (5)	22.3	< 0.001	5.2 (6.2)	0.8	0.405
GW (mm)	cephalopods	0.1	83 (3)	28.1	< 0.001	3.1 (2.7)	1.2	0.247
		0.9	118 (5)	22.7	< 0.001	5.2 (6.5)	0.8	0.427
FL (mm)	crabs	0.1	482 (59)	8.2	< 0.001	4.9 (1.8)	2.7	0.009
		0.9	537 (202)	2.7	0.010	25.7 (9.0)	2.9	0.006
GH (mm)	crabs	0.1	53 (7)	8.1	< 0.001	0.6 (0.2)	2.7	0.008
		0.9	59 (23)	2.6	0.011	2.9 (1.0)	2.9	0.006
GW (mm)	crabs	0.1	58 (7)	8.4	< 0.001	0.6 (0.2)	2.7	0.009
		0.9	65 (24)	2.7	0.010	3.1 (1.1)	2.8	0.006

3.10 Supplemental Material

3.10.1 Supplemental Figures

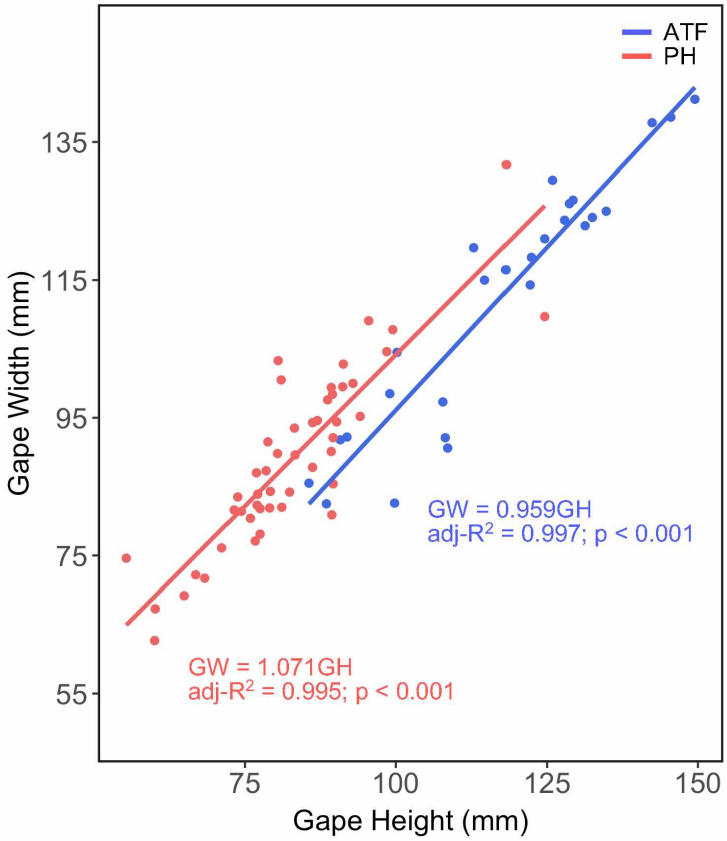


Figure S3.1 Relationships between gape height and gape width for Arrowtooth Flounder (ATF; blue) and Pacific Halibut (PH; red), Southeast Alaska (2015 to 2016).

a)

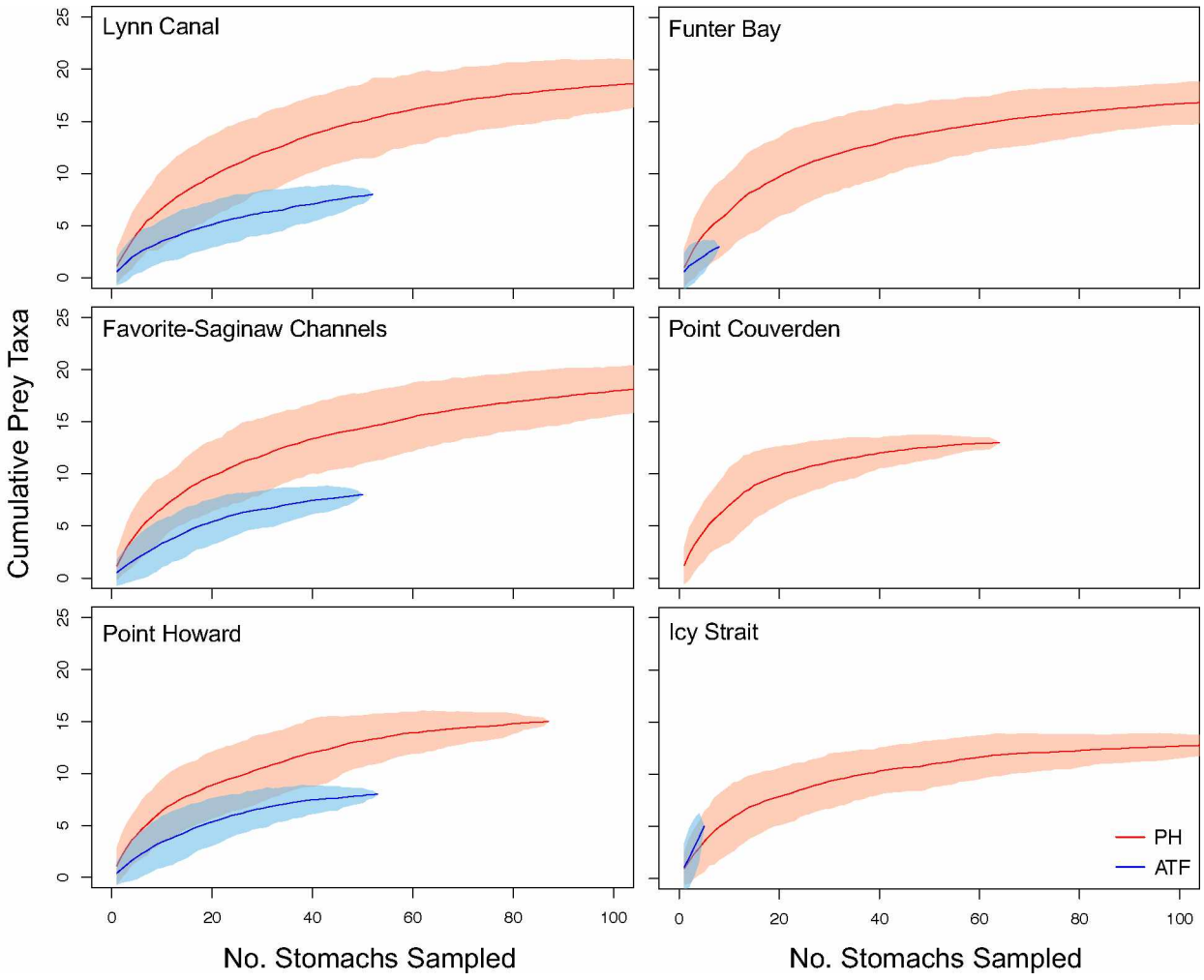


Figure S3.2 Prey accumulation curves by a) sampling site, b) fork length (cm), c) gape height (mm), and d) gape width (mm). Arrowtooth Flounder is shown in blue and Pacific Halibut is shown in red. Shaded areas indicate 95% confidence intervals.

b)

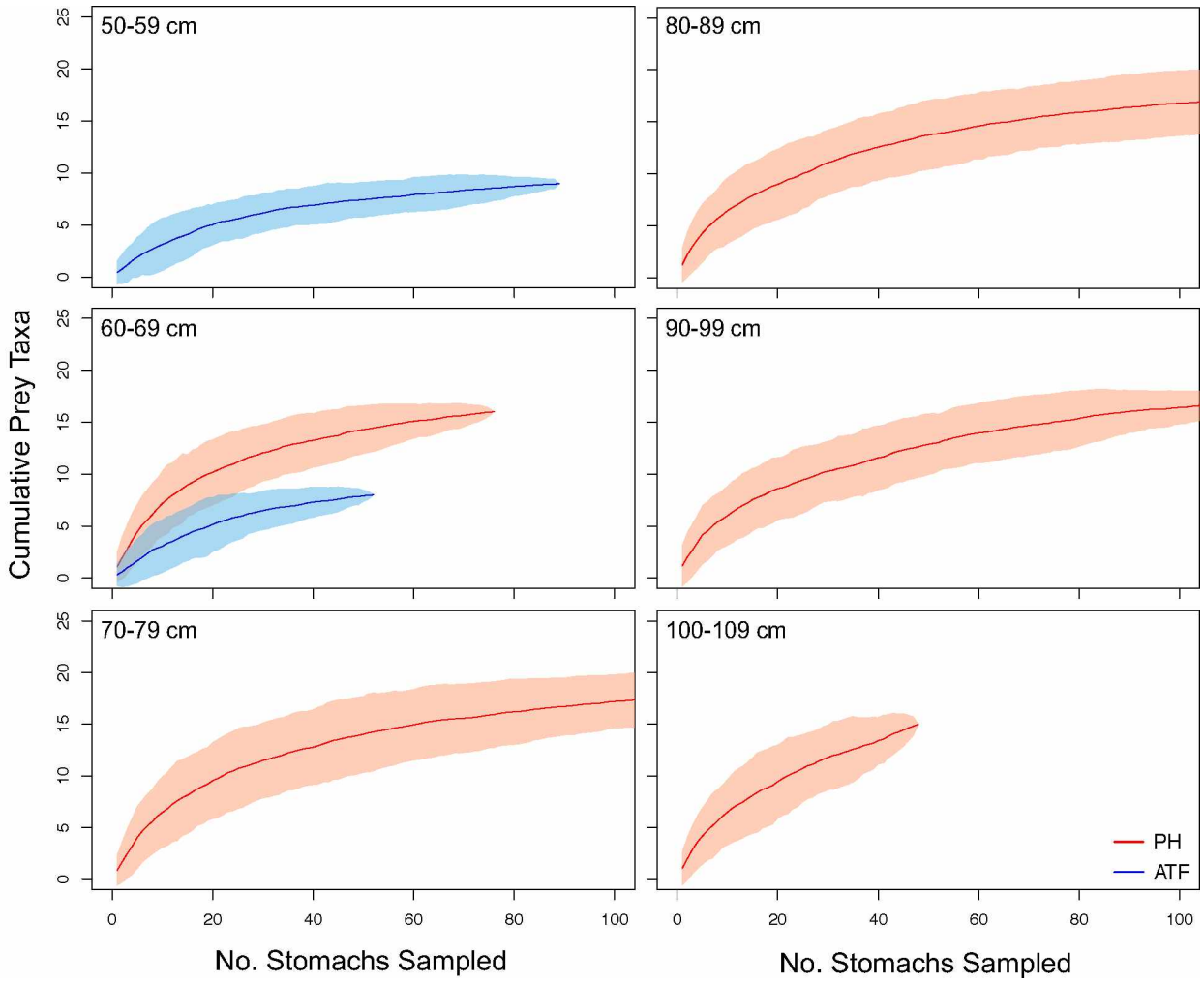


Figure S3.2 (cont) Prey accumulation curves by a) sampling site, b) fork length (cm), c) gape height (mm), and d) gape width (mm). Arrowtooth Flounder is shown in blue and Pacific Halibut is shown in red. Shaded areas indicate 95% confidence intervals.

c)

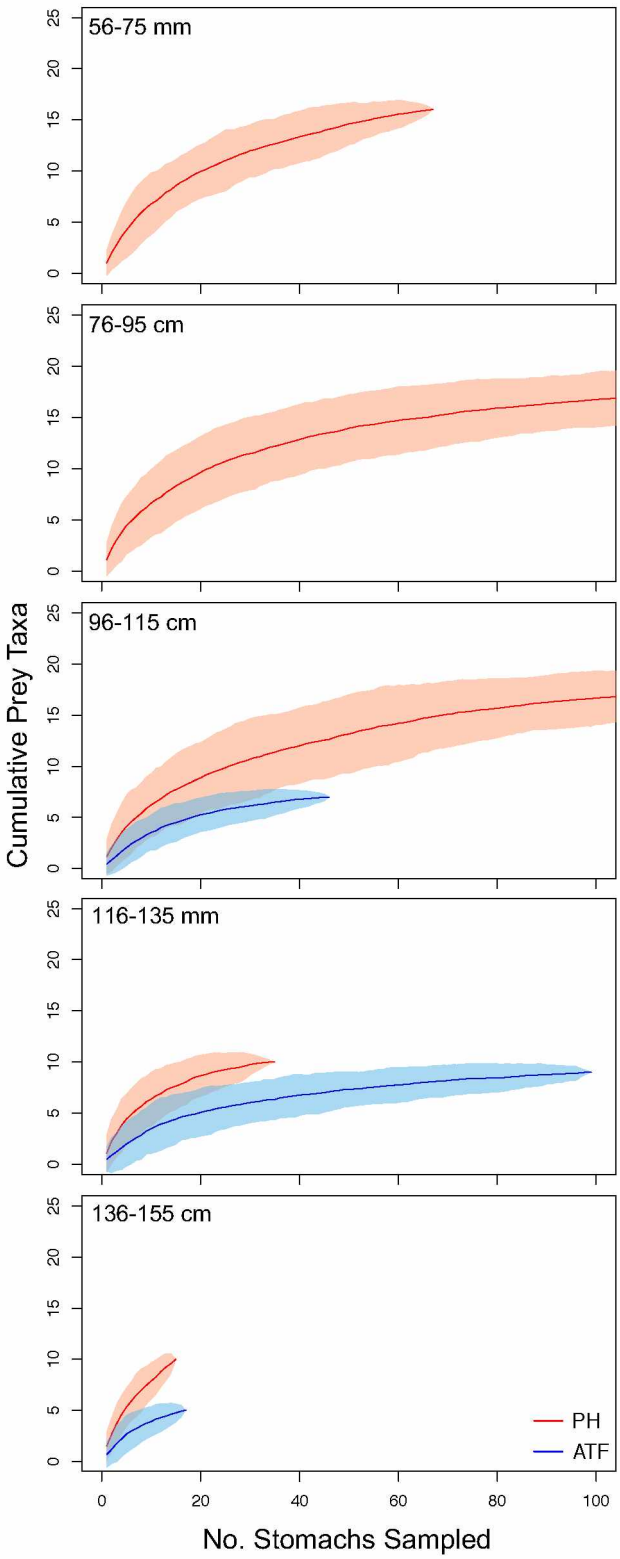


Figure S3.2 (cont) Prey accumulation curves by a) sampling site, b) fork length (cm), c) gape height (mm), and d) gape width (mm). Arrowtooth Flounder is shown in blue and Pacific Halibut is shown in red. Shaded areas indicate 95% confidence intervals.

d)

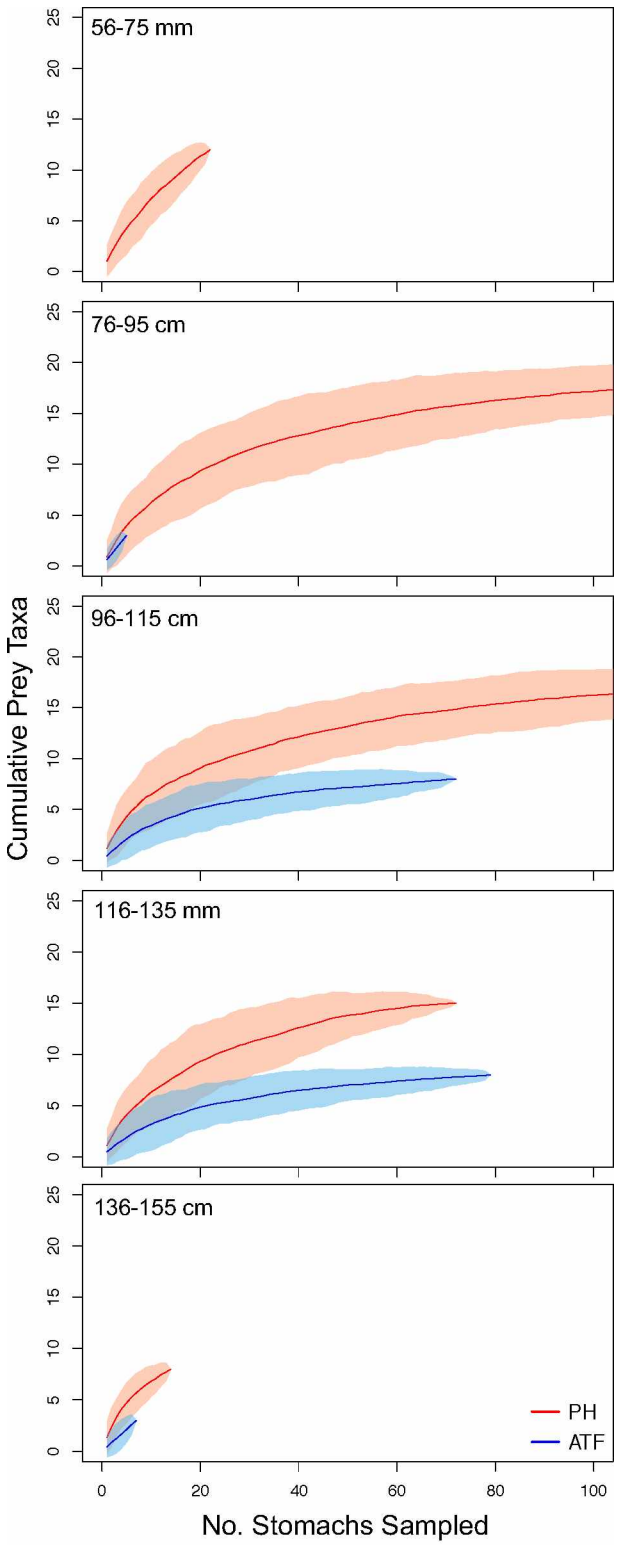
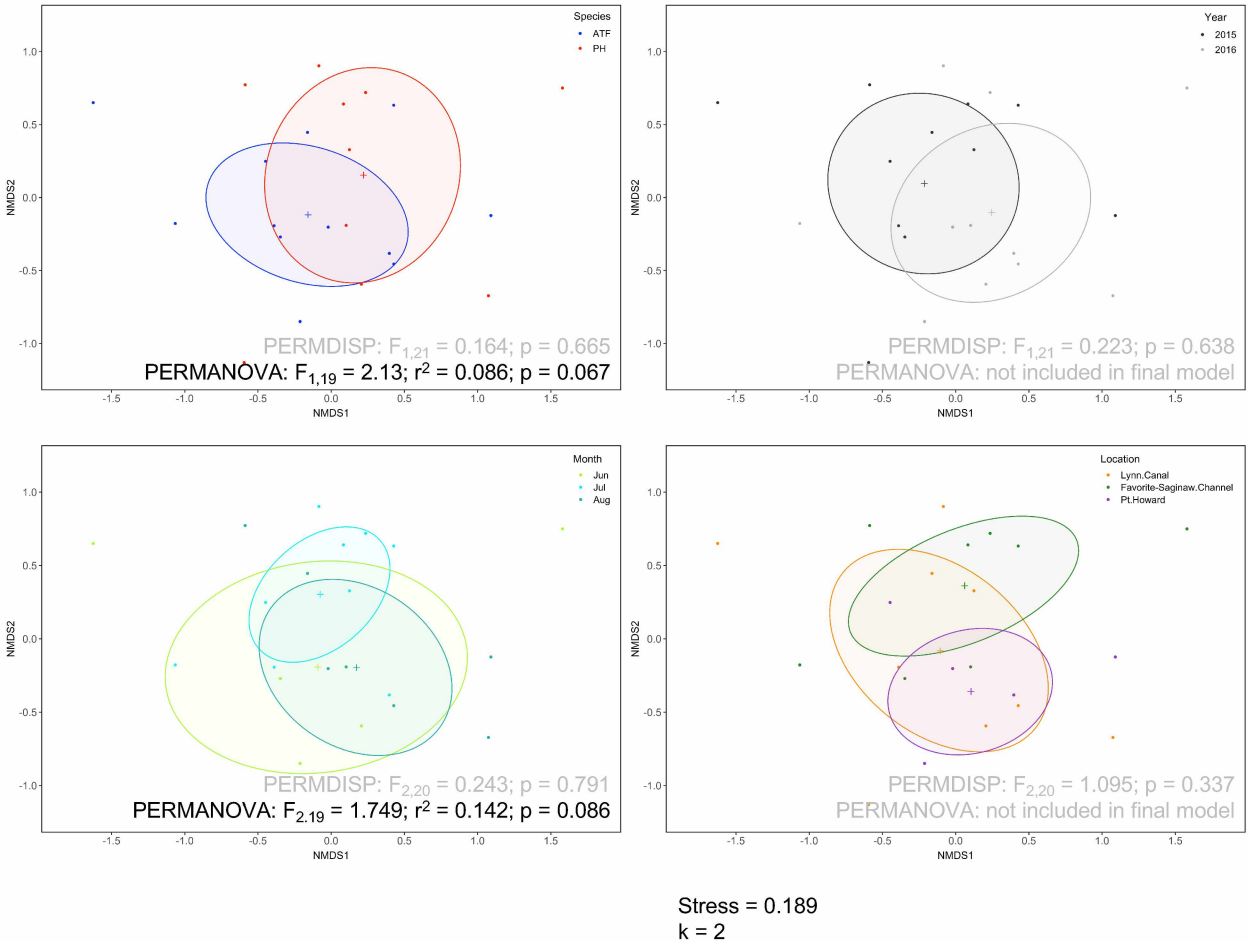


Figure S3.2 (cont) Prey accumulation curves by a) sampling site, b) fork length (cm), c) gape height (mm), and d) gape width (mm). Arrowtooth Flounder is shown in blue and Pacific Halibut is shown in red. Shaded areas indicate 95% confidence intervals.

a)



Stress = 0.189
k = 2

Figure S3.3 Non-metric multidimensional scaling plots depicting diet compositions for Arrowtooth Flounder (ATF) and Pacific Halibut (PH) in Southeast Alaska (Lynn Canal, Favorite-Saginaw Channels, and Point Howard sites only; 2015 to 2016). Individual points represent multivariate diet compositions for each unique combination of year, month, location, and size bin: a) fork lengths from 60 to 69 cm (one size bin only); b) gape heights from 96 to 135 mm; c) gape widths from 96 to 135 mm. Ellipses represent 95% confidence intervals. Stress estimates and number of dimensions (k) are listed for each size bin. Non-significant terms are shown in gray.

b)

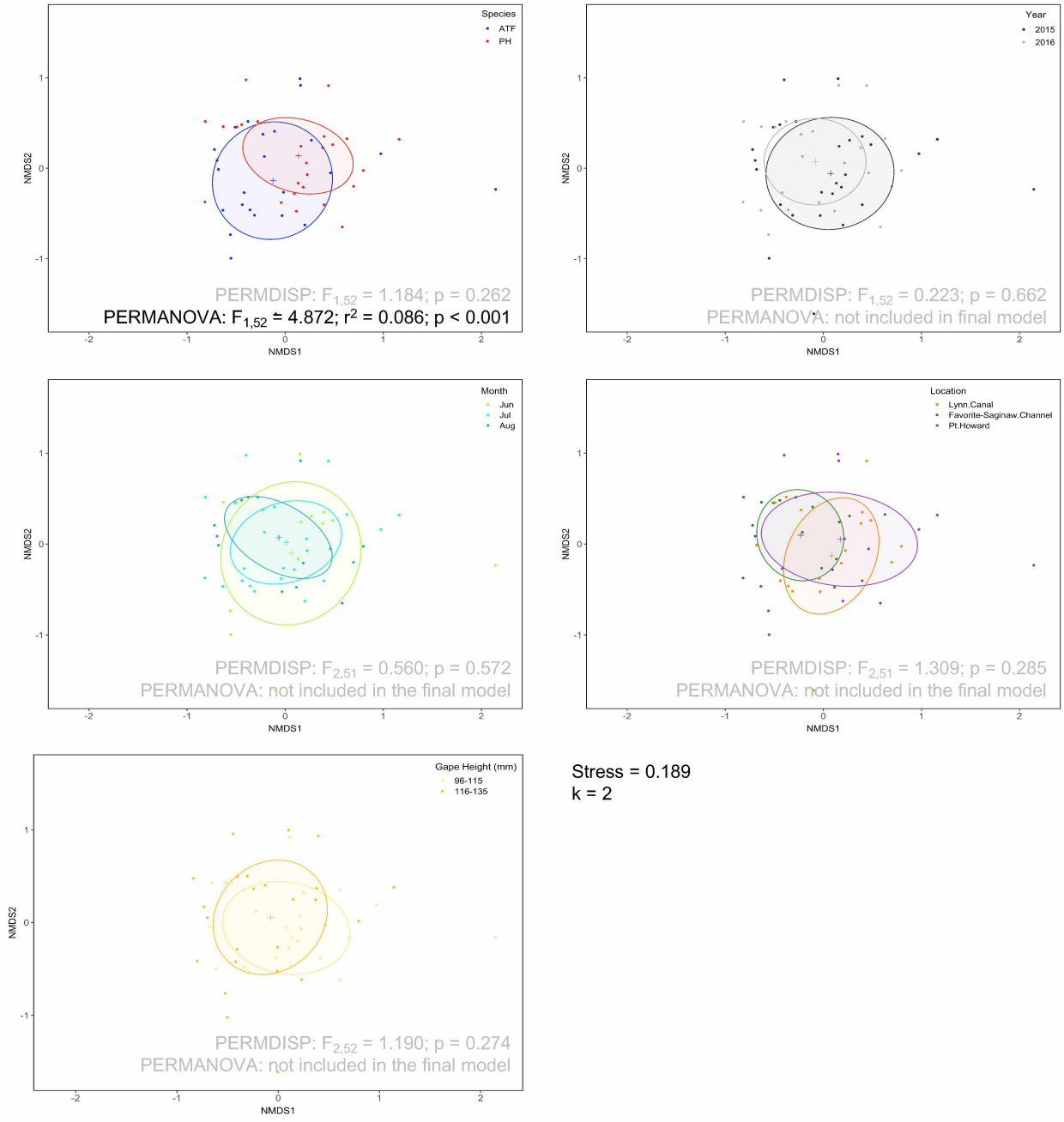


Figure S3.3 (cont) Non-metric multidimensional scaling plots depicting diet compositions for Arrowtooth Flounder (ATF) and Pacific Halibut (PH) in Southeast Alaska (Lynn Canal, Favorite-Saginaw Channels, and Point Howard sites only; 2015 to 2016). Individual points represent multivariate diet compositions for each unique combination of year, month, location, and size bin: a) fork lengths from 60 to 69 cm (one size bin only); b) gape heights from 96 to 135 mm; c) gape widths from 96 to 135 mm. Ellipses represent 95% confidence intervals. Stress estimates and number of dimensions (k) are listed for each size bin. Non-significant terms are shown in gray.

c)

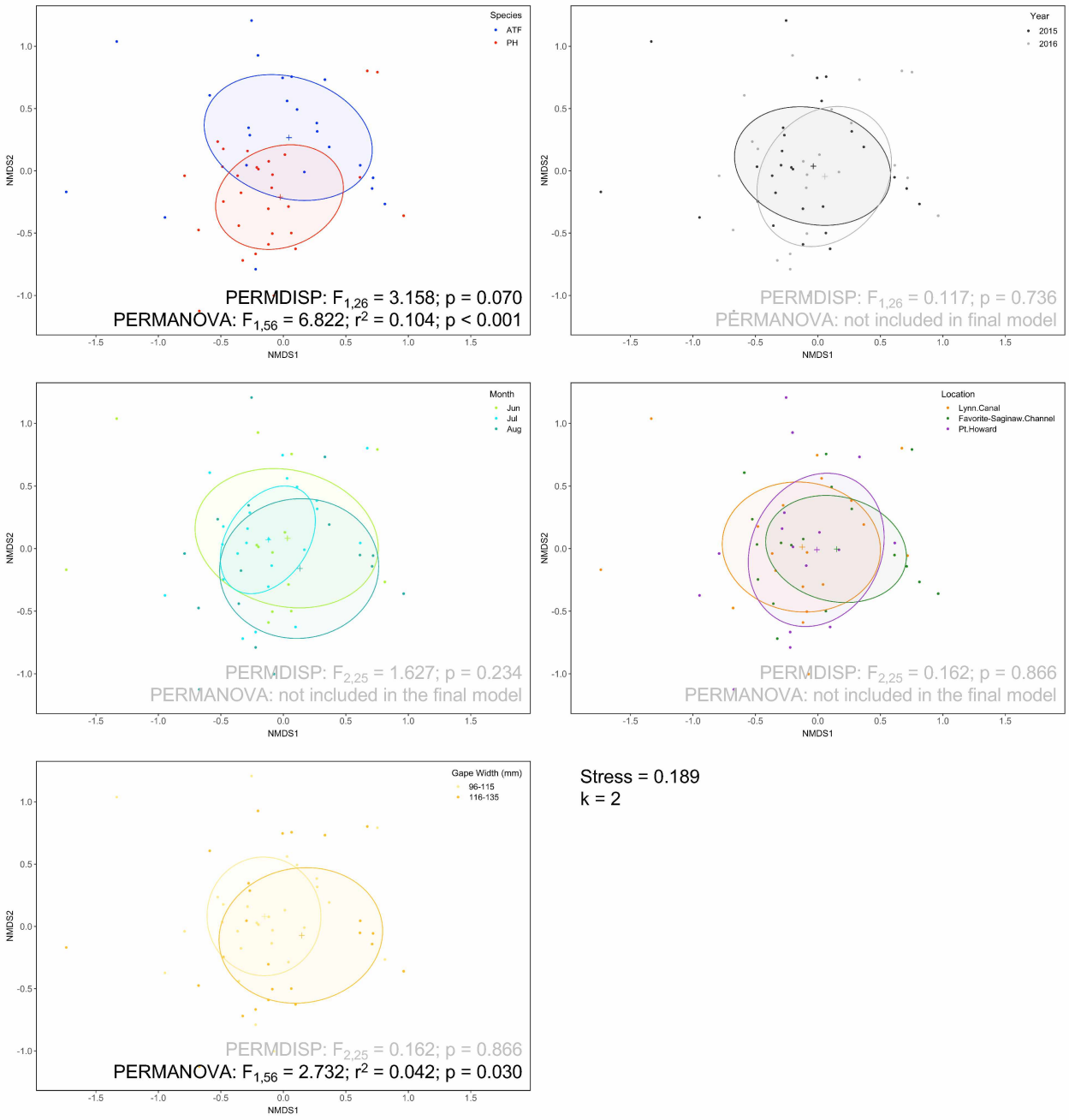


Figure S3.3 (cont) Non-metric multidimensional scaling plots depicting diet compositions for Arrowtooth Flounder (ATF) and Pacific Halibut (PH) in Southeast Alaska (Lynn Canal, Favorite-Saginaw Channels, and Point Howard sites only; 2015 to 2016). Individual points represent multivariate diet compositions for each unique combination of year, month, location, and size bin: a) fork lengths from 60 to 69 cm (one size bin only); b) gape heights from 96 to 135 mm; c) gape widths from 96 to 135 mm. Ellipses represent 95% confidence intervals. Stress estimates and number of dimensions (k) are listed for each size bin. Non-significant terms are shown in gray.

3.10.2 Supplemental Appendix: IACUC Research Approval

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 14, 2015

To:	Anne Beaudreau, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[740158-4] Resource partitioning between Pacific Halibut and Arrowtooth Flounder in Southeast Alaska

The IACUC reviewed and approved the Revision to the Personnel List referenced above by Administrative Review.

Received:	July 14, 2015
Approval Date:	July 14, 2015
Initial Approval Date:	April 20, 2015
Expiration Date:	April 20, 2016

This action is included on the July 23, 2015 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

3.10.2 Supplemental Appendix: IACUC Research Approval (cont)

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 1, 2016

To:	Anne Beaudreau, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[740158-5] Resource partitioning between Pacific Halibut and Arrowtooth Flounder in Southeast Alaska

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been approved for an additional year.

Received:	March 29, 2016
Initial Approval Date:	April 20, 2015
Effective Date:	April 1, 2016
Expiration Date:	April 20, 2017

This action is included on the April 14, 2016 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures detailed in the form 005 "Reporting Concerns".*

General Conclusions

There are a variety of benefits to understanding the direction and magnitude of food web interactions. At the most basic level, quantifying predation and the potential for competition informs us about ecosystem structure and function. When economically valuable species are involved, trophic studies improve our ability to predict abundances of harvested stocks in response to environmental change and community reorganization (Polis *et al.* 1996; Link 2002). This dissertation contributes to our scientific understanding about how ecological interactions among groundfish populations have changed through time, across space, and among different life stages in the Gulf of Alaska. Results from this work have application to fisheries management, within the region and elsewhere.

Predation and Trophic Stability in the Gulf of Alaska

Although bottom-up processes undoubtedly play a role in structuring the demersal fish community, we focused on top-down (and lateral) interactions, which may be more important in northern latitude ecosystems such as the Gulf of Alaska (*e.g.,* Francis and Hare 1994; Frank *et al.* 2006; Hunsicker *et al.* 2011). In fact, a number of studies have recognized the need for a better understanding of predator-prey interactions to improve multispecies models within the region (*e.g.,* Hollowed *et al.* 2000; van Kirk *et al.* 2010; Gaichas *et al.* 2011). A substantial shift in community composition, characterized by considerable decreases in pollock biomass and concurrent increases in predator biomass, served as the impetus for quantifying spatiotemporal changes in pollock predation. Not surprisingly, we found that Arrowtooth Flounder was responsible for the vast majority of pollock consumed by five focal predators in the Gulf of Alaska. The dominance of a single predator, when combined with synchronous consumption among other major groundfish species suggested only limited portfolio effects and some degree of trophic instability in the

region. Stability appeared to decrease with time (1990 to 2015), as synchrony in consumption among predators increased. However, predator biomass, primarily that of Arrowtooth Flounder and Pacific Cod, recently dropped to its lowest level in three decades (Zador and Yasumiishi 2018). Continuing to estimate pollock consumption and the degree of synchrony among groundfish predators would elucidate whether or not these decreases in predator biomass resulted in a greater portfolio effect following the end of our time series. Additionally, we inferred strong top-down control over pollock. Thus, we would expect an increase in pollock biomass, if recent decreases in predator biomass persist. Continued use of our predation index would inform how pollock mortality, synchrony, and trophic stability change with predator biomass. It would also be useful to track changes in pollock consumption through time, as the groundfish community in the Gulf of Alaska responds to rapid and intense climate change. Understanding how pollock mortality changes through time, in space, and under varied ecological conditions is of considerable importance because pollock are highly connected within the Gulf of Alaska food web (Gaichas and Francis 2008) and support a variety of large-scale fisheries, either through direct harvest or as prey for other economically valuable stocks.

Resource Partitioning and the Potential for Competition

Resource partitioning is a valuable tool for assessing competition, especially at broad spatial scales that are not conducive to experimental manipulation (Link and Auster 2013). It can be challenging, however, to justify the use of resource partitioning as an indicator of competition because mechanistic interpretations of niche overlap are context-specific. Substantial niche overlap may very well signify the potential for competition when habitat or prey sources cannot fully support both competitors. This scenario necessitates the division or partitioning of resources at some point in time or across space to alleviate effects of

competition. In another context, substantial niche overlap may simply represent the shared utilization of an abundant resource. This situation is plausible for flatfishes, which tend to feed opportunistically on locally abundant prey (Link *et al.* 2005). Schools of herring, for instance, may be so readily available (even if high abundances are ephemeral) that both species are able to consume relatively large quantities without competing for access. These conflicting interpretations of shared niche space demonstrate the need to account for resource availability when using resource partitioning as a proxy for competition (Ross 1986; Link and Auster 2013). However, it is extremely difficult to demonstrate that a particular resource is limiting, especially at broad spatial and temporal scales. Thus, we necessarily simplified our assessment of competition by assuming resources were limited.

We found no relationship between spatial overlap and dietary overlap for similar fork lengths of Arrowtooth Flounder and Pacific Halibut in the Gulf of Alaska. This lack of a relationship could signify an absence of competition between the two groundfish predators at broad spatiotemporal scales. Alternatively, it could be a product of missing pre-competition data (halibut size-at-age decreased well before 1990, when standardized data collection began), spatiotemporal scales that do not match those at which competition is taking place (*i.e.,* analyses conducted at too broad of scales for detection), or inappropriate comparisons by size. When we examined size-structured resource overlap in Southeast Alaska, we found evidence of trophic niche partitioning between small-bodied Arrowtooth Flounder and relatively large Pacific Halibut, both with similar gape sizes. Evidence of resource partitioning in Southeast Alaska may demonstrate ongoing competition in nearshore waters, increased detectability at finer spatial scales, or disparate interpretations according to the size metric used as a basis of comparison. An assessment of resource use by gape size class would elucidate whether or not patterns observed as part of our field study ring true throughout the Gulf of Alaska.

Making Ecological Inferences from Fisheries Data

Long-term, spatially-expansive surveys are incredibly useful when trying to answer ecological questions pertaining to highly mobile fish in the marine environment. These standardized surveys provide large quantities of data that reflect natural ecological and environmental conditions without restricting analyses to a small set of *a priori* variables. Although sampling programs prevent the isolation of specific factors, the holistic nature of observational data is advantageous for many reasons. Above all else, we (as scientists and as human beings) are unable to fully grasp the multitude of interacting and complex factors that drive ecosystem structure and function (Francis and Hare 1994). Additionally, it is difficult to preconceive the most appropriate scale with which to evaluate mechanisms of ecological change. We may infer that ecological interactions are responsible for patterns (*e.g.,* decreased prey abundances, changes in size-at-age) at the individual, short-term, or patch scale, but attribute observations to something entirely different (*e.g.,* community-level responses to environmental change) at population, long-term, or basin scales. Historical-descriptive studies help overcome this issue by allowing for assessments of population and community dynamics at a variety of scales. Finally, because population- and community-level responses to perturbation are highly variable and often characterized by considerable delays (Wilson 2006), we emphasize the need for ongoing support of long-term monitoring programs.

With limited financial resources, fisheries management must focus on select highly-connected and interdependent species that are responsible for the majority of energy flow. This includes Arrowtooth Flounder, Pacific Cod, Pacific Halibut, and Walleye Pollock in the Gulf of Alaska (Gaichas and Francis 2008). However, increased collaboration among academic scientists, agency staff, and members of the fishing industry can help supplement biological and ecological information for species, time periods, and/or locations not

encompassed by broad-scale surveys. Fishery stakeholders, for example, are decidedly invested in understanding the mechanisms that affect stock status and trends. In order to effectively leverage limited resources, disparate skill sets, and various areas of expertise, we must go beyond simple cooperation and conduct truly collaborative research involving many user groups. This is how we will develop a shared, comprehensive understanding about economically, ecologically, and culturally valuable species. Through this type of collaboration, we investigated effects of predation and competition among important groundfishes in the Gulf of Alaska. Specific contributions of this work include estimates of predation mortality that can be used as an intermediary between conventional single species assessments and full ecosystem-based fisheries management research as well as an enhanced understanding about how changing competitive interactions may impact the characteristics of important fish stocks.

Directions for Future Study

This dissertation provides additional support for top-down control in the Gulf of Alaska (*e.g.,* Gaichas *et al.* 2011; Gaichas *et al.* 2015). However, intense predation pressure and top-down processes are not uniquely important to pollock or to the Gulf of Alaska (*e.g.,* Worm and Myers 2003; Hessen and Kaartvedt 2014; Hunsicker *et al.* 2012). The methods we developed for quantifying spatiotemporal variation in consumption and trophic stability could be appropriately applied to other species and systems, as long as sufficient survey data are available. For instance, Pacific Herring are important prey for a variety of groundfish, seabird, and marine mammal predators (Surma *et al.* 2018), and are regularly sampled throughout Southeast Alaska (Hebert 2019). Quantifying variation in predation mortality further our understanding about fluctuating biomass, whereas estimates of predator diversity and trophic stability allow for inferences about predatory control on

various forage fish populations – both components providing ecosystem information for use in stock assessment and fisheries management.

Though the remaining components of our research could not provide direct evidence of competition, we believe that intense ecological interactions cannot be ruled out. Continued assessments of resource partitioning, which span periods of ecological and/or environmental change, would help elucidate whether competition can be an important driver of changing size-at-age. Recent decreases in Arrowtooth Flounder biomass (Spies *et al.* 2017) and stabilizing Pacific Halibut size-at-age (Stewart and Hicks 2017) should provide a model opportunity to do just that. Based on comparisons of broad spatial aggregations of data and fine-scale analyses, however, we assert that the use of multiple size metrics (*i.e.,* predicted gape height and gape width, in addition to fork length) and scales will be necessary to make strong ecological interpretations from such work. We also recommend that food web models, which currently rely on fork lengths or body weights to calculate predator rations (*e.g.,* Aydin *et al.* 2007), also account for variation in diet as a function of predator gape size. This will be especially important when making comparisons of prey consumed by predators with differences in allometric growth.

Finally, we believe that assessing relationships between ecological interactions and climate is an important direction for future study. Modeling predation intensity and niche complementarity as a function of environmental covariates, for instance, would be especially useful for high latitude food webs. These communities are most likely to experience compounding effects of changing climate and community and are often characterized by shifting species distributions (Ciannelli *et al.* 2013), changes in spatial overlap between predator and prey (Hunsicker *et al.* 2013), and increased predator demand (Holsman and Aydin 2015). Because climate-ecological relationships may not remain constant through time (Litzow *et al.* 2018), non-stationarity should also be considered.

These added layers of complexity should provide greater insight into the ecological mechanisms responsible for population- and community-level change across systems.

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